Diving behaviour, diet and foraging locations of the Hutton's shearwater (*Puffinus huttoni*)

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Abstract

The endangered Hutton's shearwater is endemic to New Zealand and breeds only in two alpine colonies near Kaikōura and a third colony established on the Kaikōura Peninsula. Little is known about the at sea behaviour of this species. In this thesis, I fill some of the gaps in our knowledge of the at sea behaviour and ecology of Hutton's shearwater, in order to aid its conservation. I first describe the diving behaviour of the Hutton's shearwater using Time-Depth Recorders (TDR) and compare it between the incubation and chick-rearing periods. I found Hutton's shearwaters can dive up to 35 m and for periods of up to 60 s. Incubating birds dived deeper than birds feeding chicks, and a significant difference in diving depth and dive duration was detected at different times of the day. The temporal and seasonal variation I observed in the diving behaviour suggests Hutton's shearwaters are likely to exploit different types of pelagic prey at different stages in their breeding cycle. I next examined the stable isotope composition of normal and experimentally-induced feathers to compare the breeding and non-breeding diet of the Hutton's shearwater. I found that feather isotopic compositions were not consistent with a diet based on feeding locally, but that Hutton's shearwaters were potentially consuming prey items in the area adjacent Banks Peninsula (~100 km south). I found significant segregation in $\delta^{13}C$ and $\delta^{15}N$ tail feather values between induced breeding period feathers and non-breeding periods confirming that the feathers were grown during the non-breeding period and likely from sources in the Indian Ocean, off Western Australia. Sexual differences in isotopic composition were also detected during the non-breeding period, suggesting spatial or temporal resource partitioning between the sexes while on the non-breeding grounds. I then used GPS and TDRs to track birds to

their foraging areas, determine diving depths, and estimate trip duration during the chick-rearing period. I found shearwaters travelled from their breeding grounds at Kaikōura to coastal and oceanic areas situated 125–325 km south and near Banks Peninsula, confirming the conclusions reached earlier by isotope analyses. Trip durations varied from 2 to 15 days (mean = 6), while dive depths ranged from 3 to 16 m (mean = 5.5 m). I also considered the affects of the recent earthquakes in the area and other environmental fluctuations. Finally, I present the stable isotope dietary pathway from breeding females to Hutton's shearwater nestlings. I compared the relative contribution of endogenous and exogenous resources, and found the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of natal chick feathers was significantly different to the adult feathers experimentally induced during the breeding season. This suggests that the nutrients collected by Hutton's shearwaters during the non-breeding period were predominantly used to produce the egg and consequently the hatchling and its first natal feathers but that subsequent nestling feathers became progressively similar to the local environment and induced adult feather samples as the adults fed their chicks and as the season progressed. Overall, my study provides a snapshot of the Hutton's shearwater at sea diving behaviour, diet and foraging locations. Based on my results, the Hutton's shearwater demonstrates temporal and seasonal variation in diving behaviour, they forage outside of Kaikōura region and at greater distances than previously thought, and they are predominantly endogenous breeders early in the breeding season, but then rely on exogenous resources as their chicks mature. With on-going research into the changes in the marine environment and through further monitoring of the Hutton's shearwater (e.g., interaction with commercial fisheries), the future conservation and protection of this endangered seabird can be implemented.

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Hutton’s shearwater rafting and flying off the Kaikōura Peninsula, 20 September 2014 (photo by Della Bennet).

Chapter 1
General Introduction

Procellariiforme seabirds

The order Procellariiformes or tube-nosed seabirds (including albatrosses [Diomedeidae] storm petrels [Hydrobatidae], diving petrels [Pelecanoididae], and shearwaters, fulmars and prions [Procellariidae]) (Harper & Kinsky 1978; Warham 1996; Bocher et al. 2000) are a highly successful group of pelagic birds that are distributed worldwide, not only in the number of species but also in the number of individuals (Cooper et al. 1991; Warham 1996; Bocher et al. 2000; Jodice & Suryan 2010). Most of these species are found in the Southern Hemisphere (Davies et al. 2010). Procelleriiforms are top marine predators and are important in maintaining oceanic food webs (Neves et al. 2012). It has been suggested that species in the Procellariiformes provide a valuable tool as indicators of marine environmental change, prey population levels and general ecosystem health (Furness & Camphuysen 1997; Schumann et al. 2008; Croxall et al. 2012; Neves et al. 2012).

Procellariiformes are highly adapted to the marine environment, showing various ecological and physiological adaptations to a pelagic life history (Warham 1996). They spend their life predominantly at sea, only returning to land to breed (Harper & Kinsky 1978; Cooper et al. 1991; Croxall et al. 2002; Shaffer et al. 2006; Jodice & Suryan 2010). Most species are adapted to long-distance flying, with wing-spans varying from as little as 32 cm in the least storm-petrel (*Oceanodroma microsoma*) to

3.5 m in the snowy albatross (*Diomedea exulans*) (Bried et al. 2003; Onley & Scofield 2007). Foraging flights often cover long distances over a period of several days (Fayet et al. 2015; Dias et al. 2016; Avalos et al. 2017). During the non-breeding period, many species also make long trans-equatorial migratory journeys (e.g., sooty shearwater [*Puffinus griseus*] return migration ~64,037 km) (Shaffer et al. 2006; Yamamoto et al. 2010; Dias et al. 2011). Breeding typically involves laying only a single egg per breeding season in either a surface nest, burrow or crevices, followed by a long incubation and chick-rearing period (Warham 1990, 1996). Depending on the species, fledged birds remain at sea for an extended period of time (2–9 years) before returning to their natal area to breed (Hamer et al. 2002). Many species are extremely long-lived, with some of the largest albatross having lifespans of >50 years (Foote et al. 2010; Lecomte et al. 2010).

Due to their low reproductive rate, variation in breeder survival and the recruitment of pre-breeders can have a major impact on population health and persistence (Phillips et al. 2017). Age, foraging experience and sex have been seen to contribute to population survival and reproduction (Daunt et al. 2007; Regular et al. 2013; Jaeger et al. 2014; Phillips et al. 2017). For example, young male wandering albatrosses (*Diomedea exulans*) change foraging areas when they join the breeding population and progressively forage further south with increasing age. This behavioural change can lead to lower nest attendance, female desertion, and lower probability of reproducing over the following years (Jaeger et al. 2014). In other seabirds, such as European shags (*Phalacrocorax aristotelis*), foraging efficiency increased with age and experience when provisioning chicks, especially during the late breeding period

when resource availability was poor (Daunt et al. 2007). Understanding how a species responds to changing conditions can assist in its conservation.

Threats to oceanic seabirds

Seabirds are one of the most threatened group of birds, and many species continue to decline (Croxall et al. 2012). Currently, the most threatened species are in the Sphenisciformes and Procellariiformes which represent around 43% of all seabirds (Croxall et al. 2012). The situation in New Zealand is particularly perilous, as it has double the number of threatened seabird species compared to any other country (Croxall et al. 2012). New Zealand also has the most endemic breeding species of seabirds, and has the highest conservation concern for breeding and non-breeding species combined.

Pelagic seabirds (especially albatrosses and large petrels) appear to be more threatened than coastal species (Croxall et al. 2012). Historically, most species were subject to predation predominantly by native avian predators (including gulls and skuas), but their survival is now threatened by a range of introduced mammalian predators (including hunting by humans), and anthropogenic impacts such as commercial fisheries by-catch, pollution, and climate change (Marchant & Higgins 1990; Warham 1996; Croxall et al. 2012; Hervías et al. 2013). Procellariiformes are highly vulnerable to non-native mammalian predators, as they have limited defences against this predatory guild. It is thought that native avian predators may have favoured behavioural changes such as being nocturnal, nest burrowing and the use of remote island areas, but these traits now make them susceptible to mammalian predators (Warham 1996).

To understand the current pressures and future survival of a species, a baseline account of current impacts are required (Rollinson et al. 2014; Mattern et al. 2017). Unfortunately, the monitoring of seabird species raises a lot of challenges as they spend their life predominantly at sea. However, the development of tracking technology means it is now possible to collect detailed information on their migration, moult, diet and foraging behaviour (Shaffer et al. 2006; Meier et al. 2016; Shoji et al. 2016). Fundamental to implementing effective conservation actions, such as minimising conflict with fisheries or delimiting the boundaries of marine reserves, is an understanding of the foraging behaviour and movements of a species while at sea. In this thesis, I use a variety of approaches, including at sea tracking and stable isotope analyses, to describe the foraging behaviour and movements of the Hutton's shearwater (*Puffinus huttoni*), near its only breeding location near the town of Kaikōura, New Zealand. I begin by reviewing the approaches I will use in this study.

Study methods

Approaches to studying foraging behaviour of seabirds

There are numerous approaches to threatened and endangered species management (Miskelly et al. 2009; Lascelles et al. 2012; Meier et al. 2015; Meier et al. 2016; Robertson et al. 2017). Often the main issue affecting a species' survival is not entirely clear, and a proactive approach is needed to test the best management strategies. For instance, in the North Island kōkako (*Callaeas cinereus*), control of introduced mammalian predators was deemed more important in limiting population size than food competition (Innes et al. 1999). Whereas, in the case of the Hutton's

shearwater, predatory control may assist species conservation but may not address other contributing factors affecting the species' survival, including marine food resources (Cuthbert 2002).

The best method of observation needs to complement the main focus of the study. Whether by ship-based observational approach (Bartle 1974; Camphuysen et al. 2004), fisheries by-catch (Žydelis et al. 2009; Bellebaum et al. 2013; Bond & Lavers 2014; Fossette et al. 2014), analysis of beach-wrecks (Harrow 1965; Bartle 1974), and crashed birds (Rodriguez et al. 2012), or even through stomach content analysis (Colabuono & Vooren 2007; Bester et al. 2011; Neves et al. 2012), each of these methods have inherent issues and biases. For example, dietary studies may obtain samples from either dead birds (beach-wrecked or fisheries by-catch) (Colabuono & Vooren 2007) or by stomach flushing/regurgitation (Reid et al. 1997). This latter method can be highly invasive depending on the species involved and requires the capture and manipulation of the bird (chick or adult). Some species cannot be induced to regurgitate easily and only part samples can be collected, as in the case of the diving petrels which require gastric lavage (water off-loading). In contrast, albatross chicks can be inverted over a bucket and have their stomach massaged shortly after feeding to obtain their full sample (Reid et al. 1997; Phillips 2006; Bester et al. 2011). Even if regurgitates can be collected readily, due to the nature of the digestive process, little soft tissue remains intact and prey often cannot be identified. Alternatively, hard structures are more resistant to digestion and can lead to over-estimation of their importance in the diet (e.g., cephalopod beaks, eye lenses, and otoliths) (Duffy & Jackson 1986; Colabuono & Vooren 2007; Neves et al. 2012).

With the rapid development of technology, alternative approaches are now available. In particular, the development of Time-Depth Recorders (TDRs), Global Position System (GPS) and Stable Isotope Analysis (SIA) means it is now possible to track birds at sea, assess their behaviour and investigate dietary preference.

Time-Depth Recorders (TDR)

Diving behaviour is a major component of seabird foraging activity. Having an understanding of a species' foraging ability and potential constraints, ultimately link to other aspects of its biology and ecology (e.g., reproductive success, food web interaction, and population stability) (Shoji et al. 2015). However, observing the foraging of birds at sea and under the surface becomes difficult especially in deep-diving species. Early investigations of maximum diving depths in marine birds started with single-use lightweight capillary dive gauges (CDG) (Ropert-Coudert & Wilson 2005; Taylor 2008). These devices indicated the maximum dive depth reached by dissolving and providing a measurable line in icing sugar filled tubes. CDG were relatively accurate, especially when recovered within 48 h, but provided limited information on shallower dives and variation in dive depths (Elliott & Gaston 2009).

With the miniaturisation and waterproofing of electronic tracking technology, Time-Depth Recorders (TDR) are becoming more available to deploy on smaller bird species and cost-effective (Wilson & Vandenabeele 2012; Navarro et al. 2014). These units can track multiple diving records during a single foraging trip of an individual and record dive duration, dive frequency and environmental conditions (e.g., water temperature, time of day, dive duration) (Rollinson et al. 2014; Shoji et al. 2016). TDRs have been deployed on several species of Procellariiformes to provide a

detailed description of their diving behaviour, but similar information is still lacking on species like the Hutton's shearwater (Navarro et al. 2014; Dunphy et al. 2015). It has been suggested that some of the deepest diving birds may be some of the smallest species (Navarro et al. 2014).

Global Positioning System (GPS)

The marine environment is a large and complex ecosystem, with variation due to depth, currents, temperatures, and productivity, and it is inhabited by a variety of organisms that are linked through different trophic food webs (Waite et al. 2007a; Waite et al. 2007b; Chiswell et al. 2015). For a seabird searching for food, this variation leads to unpredictable prey and ephemeral conditions (Boyd et al. 2016), and thus the requirement to travel long distances to forage. With the development of lightweight, low cost, small, rechargeable Global Positioning Systems (GPS), it is now possible to track individual flight paths and identify foraging areas of seabirds in great detail (Shaffer et al. 2006; Bouten et al. 2013; Tew Kai et al. 2013). GPS trackers allow a researcher to pinpoint the location of a bird at regular time intervals and as a result, various ecological and biological questions can be addressed for the first time that in turn aid in a species' management (Latham et al. 2015). For example, by deploying GPS trackers, we can investigate the characteristics of an area used by a species (e.g., bathymetry, chlorophyll *a* concentrations, zones of up-welling), the distance traveled during different phases of the breeding season, the variability of each foraging trip (short or long) and to identify sexual segregation in habitat use (Avalos et al. 2017; Matsumoto et al. 2017). Knowledge gained can be used to predict how seabirds may respond to climate change, whether they interact with fisheries, and to identify any other environmental factors that may affect population size (Guilford

et al. 2008; Tew Kai et al. 2013; Grémillet et al. 2014; Avalos et al. 2017). For example, ring recoveries led to the hypothesis that Manx shearwaters (*Puffinus puffinus*) used waters south of their colony and in waters frequented by commercial sardine fisheries, but this pattern was not observed during a GPS tracking study (Guilford et al. 2008). Alternatively, with local area knowledge of foraging sites and the ability to estimate prey type in relation to main core fish species of that area, the spatiotemporal prey preference of the Cape gannets (*Morus capensis*) was established by comparing the feeding location to the local fisheries-take within the Benguela upwelling (Tew Kai et al. 2013).

Advantages and disadvantages of tracking technology

The application of tracking technology has come a long way and now allows more focused research to be undertaken on smaller species through the reduction in tracker size and the increase in storage capacity (Wilson & Vandenabeele 2012; Navarro et al. 2014). However, the ability to acquire information comes with several costs, including ethical issues (e.g., stress from human handling, immobility from device attachment, reduced foraging or grooming ability), loss of equipment or tracked individual, and equipment failure (battery or waterproofing) (Hawkins 2004; Vandenabeele et al. 2012; Berlincourt & Arnould 2015; Matsumoto et al. 2017). For example, short-tailed shearwaters (*Puffinus tenuirostris*) were tracked over three breeding seasons (2012–13) using GPS units, but the loss of equipment, unit failure and inability to recapture all individuals meant that only 50/102 loggers were recovered (Berlincourt & Arnould 2015). Use of tracking devices have also been associated with nest desertion, extended trip duration, incubation or chick abandonment and mortality (Falk & Møller 1995; Phillips et al. 2003; Thaxter et al.

2016). For example, backpack harness attachment caused increased foraging effort and mortality in Gibson's (*Diomedea gibsoni*), and Antipodean (*D. antipodensis*) albatrosses, south polar skuas (*Catharacta maccormicki*) and northern fulmars (*Fulmarus glacialis*), whereas leg-loop or tape attachment had little effect (Falk & Møller 1995; Walker & Elliott 2006; Mallory & Gilbert 2008). Alternatively, although no major impacts were detected during a GPS tracking study on the greater skua (*Stercorarius skua*) using wing harnesses during the breeding season, catastrophic losses occurred during migration and over the winter period (only 1/20 birds returned) (Thaxter et al. 2016).

Careful consideration must be taken when assessing a species for tracking and to consider the most appropriate attachment method given its morphological and behavioural characteristics (Mott et al. 2015). Contrasting effects were detected between lesser black-backed gulls (*Larus fuscus*) and great skuas, in which skuas, but not gulls were negatively affected by the harness attachment (Thaxter et al. 2016). The conservation status of the targeted species and the benefits gained by using biologging, especially in declining or rare species, should also be carefully assessed (Wilson & McMahon 2006; Casper 2009; Bodey et al. 2017). Studying a similar species (e.g., body morphology, shape and ecology) and extrapolating to a focal species does not necessarily provide an appropriate result (Thaxter et al. 2016). It may be more productive to study some individuals of a threatened or endangered species than to ignore a knowledge gap (Casper 2009; Bodey et al. 2017).

Consideration of potential impacts, when assessing the equipment, should include factors such as the weight, style and size of the device. The current guidelines are to

not exceed 3%–5% of the individual's body mass (Phillips et al. 2003), but this may be too simplistic as variation within and between the energy budgets will differ among species. The attachment of a logger weighing 3% of a bird's body weight does not equate to an increase of 3% in-flight energy but instead may range from 4.76 to 5.71% without accounting for device drag (Vandenabeele et al. 2012). Thus, it is important to assess an animal's lifestyle and deploy equipment which causes the least negative impact as practicable (Casper 2009).

Stable Isotope Analysis (SIA)

Stable isotope analysis has become a powerful ecological tool to analyse photosynthetic pathways (Marshall et al. 2008), food webs (Post 2002; Montoya 2007; Inger & Bearhop 2008) and to investigate the behaviour of pelagic seabirds whilst away from the colony. Not only can it be used to investigate the diet and energy sources of a particular species, but also to understand feeding locations and migratory patterns (Quillfeldt et al. 2010; Cherel et al. 2016; Meier et al. 2016; Polito et al. 2017). An organism generally utilises a lower trophic level, whether it be inorganic carbon, nitrogen, oxygen, sulphur and/or hydrogen from the soil, water, or from a lower trophic structure, for example, plant or phytoplankton (Peterson & Fry 1987; Michener & Kaufman 2007; Inger & Bearhop 2008). Stable isotopes are elements that are subtly different in atomic mass through the number of neutrons present (Inger & Bearhop 2008; Ramos & González-Solís 2012). As the consumer utilises these resources, the ratio of light to heavy isotopes alter as they pass through the varying metabolic pathways, thereby altering the isotopic ratio or fraction within the organism's tissue (whole organism or specific part).

Various tissues can be used for isotopic analyses, including blood, tissues (including liver, kidney, muscle), egg components (shell, yolk, albumen and membrane), feathers and stomach contents to analyse the diet, growth and nutritional status of a species, as well as various spatiotemporal events (Cherel et al. 2002; Hobson 2007; Montoya 2007; Sears et al. 2009; Polito et al. 2017). Once assimilated into the tissues, these materials are inert and do not undergo radioactive decay over time (Hobson 1999a; Inger & Bearhop 2008; Ramos & González-Solís 2012).

Carbon (13C:12C expressed as $\delta^{13}C$) and nitrogen (15N:14N as $\delta^{15}N$) are elements commonly used in isotopic studies of seabird ecology and food webs (Inger & Bearhop 2008; Bond & Jones 2009). For example, blood provides an accurate representation of the current diet and health of a bird, including variation in foraging behaviour and prey choice. This was seen in the chick provisioning behaviour of the short-tailed shearwater (*Puffinus tenuirostris*), which alternated between long-distance foraging on Antarctic fish to maintain adult body mass and short-distance foraging in Australian coastal waters to provision chicks with crustaceans (Cherel et al. 2005b). Alternatively, the isotopic composition of feathers can be used to infer the food resources consumed at the time the feather was constructed (Hobson & Welch 1992; Hobson 2007; Inger & Bearhop 2008). It is also possible to infer the place of moult when feathers are compared to the various food sources within their winter foraging grounds (Hobson & Welch 1992; Hobson 2007; Inger & Bearhop 2008). When birds moult at the end of the breeding season, their replacement feathers are formed from the late seasonal prey, incorporating a local isotopic signature which remains until the next year's moult (Hobson & Welch 1992; Fry 2006). This method

is less invasive and less stressful on the bird than taking blood and more ethically acceptable (Labbé et al. 2013).

Isotopic signatures of feathers reflect the diet during the moult, and for many seabirds, this occurs during the non-breeding period (Cherel et al. 2000; Cherel et al. 2006; Meier et al. 2016). Ratios of carbon and nitrogen in an animal's tissues directly relates to the isotopic composition of the consumed prey tissues (Cherel et al. 2000). By comparing the isotopic composition of both the animal and its potential food items, and using an appropriate fractionation model (Hobson 1995; Bearhop et al. 2002; Post 2002; Caut et al. 2009), it is possible to estimate the likely components of an animal's diet (Phillips & Gregg 2003). Food web studies have used these naturally occurring isotopes to investigate consumer-prey trophic interactions as the isotopic ratios behave in a predictable way (Peterson & Fry 1987; Hobson & Welch 1992; Bearhop et al. 2002; Fry 2006). SIA provides a diverse and rigorous method to investigate varying aspects of avian diet and behaviour (e.g., migration), but for a robust evaluation, potential prey items need to be collected from the foraging environment to construct an accurate baseline of $\delta^{13}C$ and $\delta^{15}N$ values (Militão et al. 2013). Fractionation values are determined by subtracting the isotopic ratio of the prey tissue from the isotopic predator tissue composition (Minagawa & Wada 1984; Hobson & Clark 1992b). By using fractionation factors or step-wise enrichment of 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ between predator and prey, it is possible to infer the trophic levels and consumed protein of the food. This isotopic ratio can indicate different foraging sites through the differentiation of carbon pools, such as between offshore and inshore food webs (Hobson 1993; Hobson et al. 1994; Cherel et al. 2005a; Caut et al. 2009).

Moult analysis by stable isotope analysis

SIA is one effective tool to identify prey choice during feather growth. Sampling of primary or rectrix feathers has been used in numerous studies to provide estimates of breeding and non-breeding isotopic ratios (Hobson 1999b; Quillfeldt et al. 2008; Jaeger et al. 2009; Navarro et al. 2009; Wiley et al. 2010; Dunlop 2011; Labbé et al. 2013; Cherel et al. 2014). For example, in bridled terns (*Onychoprion anaethetus*) a significant difference was seen between the isotopic signature of the original rectrix feathers obtained after birds returned from migration (Labbé et al. 2013) and the regrown feathers sampled at various times during the breeding season, indicating a change in $\delta^{15}N$ and $\delta^{13}C$ ratios from the different foraging locations and prey choice. Labbé et al. (2003) then compared these results against historical stable isotope primary producer and consumer data (seagrass, algae, plankton and larval fish) collected by other studies (between 2003–07). Unfortunately, the confounding effects of changing climate temperatures, variation in oceanic carbon and nitrogen levels and El Niño/La Niña effects were not taken into account (Kudela & Chavez 2000; Kaeriyama et al. 2004) highlighting the need to assess the results of SIA carefully.

SIA has now been applied to a number of seabirds, with an indication of considerable variation from species to species, For example, SIA of feathers of blue petrels (*Halobaena caerulea*) showed that the adults moulted within the same location as where they breed and feed their chicks, illustrating no variation in winter migratory foraging signature (Cherel et al. 2002). In contrast, the Mediterranean (*Puffinus yelkouan*) and Balearic (*Puffinus mauretanicus*) shearwaters moult and replace their first primary feather from different regions depending on their migratory pattern

(Aegean-Black Seas, West Mediterranean Sea or within the North Atlantic Ocean) showing spatio-temporal variation (Militão et al. 2013), whereas the analysis of the South Georgian (*Pelecanoides georgicus*) and the common (*P. urinatrix*) diving petrels illustrated no dietary segregation between the two species during their moult (Bocher et al. 2000).

Advantages and disadvantages of SIA

SIA requires little manipulation of the system and generally provides the ability to test an item without affecting the organism or environment nor altering or influencing the sampled item's composition (Montoya 2007). Nevertheless, it is important to define and assess handling and sample preparation procedures in order to prevent contamination (McCutchan et al. 2003; Bontempo et al. 2014). Stable isotope analysis is less invasive compared to stomach content analysis (regurgitation or dead specimen) and can provide a long-term estimate of diet rather than a snapshot of the previous days' prey choice (Cherel et al. 2007; Michener & Kaufman 2007; Richoux et al. 2010). Depending on a prey item's composition, digestion rate can vary, and certain hard parts of a prey species (e.g., insect carapace, fish bones, teeth and scales) can remain for very long periods without being assimilated (Whitledge & Rabeni 1997; Michener & Kaufman 2007). By relying on stomach content analysis alone, an overestimation of prey choice may occur as species like cephalopods can last within the gut of a predator for weeks or months (Cherel et al. 2000).

One disadvantage of stable isotope analysis is that the different tissues hold different combinations of total C:N ratio (McCutchan et al. 2003; Cherel et al. 2008; Bond & Jones 2009) and so cannot contain the full representation of the individual's diet. This

method is not without issues in collecting, preparing and processing samples, including removal of feather oils and in some instances the extraction of lipids from blood and tissue (Kojadinovic et al. 2008b; Kojadinovic et al. 2008a; Paritte & Kelly 2009). For example, Paritte and Kelly (2009) reviewed 11 different cleaning agents recommended for removing oils from bird feathers. The most common was 2:1 chloroform:methanol, followed by a detergent, but in some cases, no cleaning is performed at all. As a result, caution should be used when comparing results between species, particularly if different methods of cleaning and preparation were used.

More researchers are now undertaking feeding studies that incorporate the effects of stress and fasting, fractionation mixing models and compound-specific isotopic analysis (Hobson & Clark 1992b; Kempster et al. 2007; Bauchinger et al. 2010; Ramos & González-Solís 2012; Doi et al. 2017). For instance, a nutritional stress study on juvenile song sparrow (*Melospiza melodia*) showed the effects of physiological stress through smaller physical size, poorer growth and brain development but no effect was detected in $\delta^{15}N$ and $\delta^{13}C$ composition values of whole blood, liver, muscle or feathers (Kempster et al. 2007). These results indicated a potential nutritional stress threshold. In contrast, extreme stress elevated $\delta^{15}N$ values in fasting post-incubating Ross' geese (*Chen rossii*), moulting king penguins (*Aptenodytes patagonicus*) and an enrichment of $\delta^{13}C$ was detected in cold-exposed zebra finches (*Taeniopygia guttata*) (Hobson et al. 1993; Cherel et al. 2005c; Bauchinger et al. 2010). Recent meta-analysis of fasting experiments found an increase in $\delta^{15}N$ over the fasting period that was largely explained by the nitrogen and energy metabolism, but no predictor variables accounted for the variation in $\delta^{13}C$ (Doi et al. 2017).

The ratios of $\delta^{15}N$ and $\delta^{13}C$ are fairly predictable and will reflect the prey isotopic contribution when compared to a known diet (Post 2002; McCutchan et al. 2003; Layman et al. 2012), but when average fractionation factors from other studies are used to infer trophic level and energy source (Post 2002; McCutchan et al. 2003), large variation in trophic enrichment can confound mixing models (Martínez del Rio et al. 2009). Fractionation factors vary between tissues of one species, between species and among diets (Caut et al. 2008; Caut et al. 2009). Many studies are using published fractionation factors (e.g., average value from a larger review) as it can be expensive and impractical to determine fractionation factors experimentally for many species, and consequently, inappropriate fractionation values are being used (McCutchan et al. 2003; Caut et al. 2008; Caut et al. 2009). These studies use estimated fractionation factors from terrestrial or captive species and apply them to wild seabirds (Hobson & Clark 1992a; Bearhop et al. 2002; Caut et al. 2009). For example, the isotopic fractionation values determined from mallards (*Anas plathyrhynchos*) and between falcons (*Falco* spp.) feed on Japanese quail muscle (*Coturnix japonica*) were used to determine the contribution of diet in the production of snow goose eggs (Hobson 1995; Gauthier et al. 2003). Alternatively, Caut et al. (2008) found the most accurate values were obtained from diet-dependent discrimination factors (DDDFs) and applying a source-partitioning mixing model called IsoSource (Phillips & Gregg 2003).

Isotopic research is now incorporating compound-specific analysis (e.g., amino acids) to increase the resolution of foraging studies and to investigate underlying physiological assumptions (Boecklen et al. 2011; Steffan et al. 2013). In particular,

phenylalanine and glutamic acid are proving to be effective in estimating trophic position, especially when compared to the large variability in bulk ^{15}N fractionation factors (Steffan et al. 2013). For example, when herbivores (trophic level 2) and carnivores (trophic levels 3 and 4) were fed controlled diets, and the bulk ^{15}N values were compared, no distinguishable variation was detected between the trophic levels, whereas the amino acid trophic fractionation factor for $\Delta^{15}N_{glu\text{-}phe}$ was consistently around +7.6 ‰ across all trophic levels (Steffan et al. 2013). This is because essential or source amino acids (e.g., phenylalanine) are assimilated from the diet to the consumer without any alteration (metabolic or physiological) and reflect the composition of the primary producer community at the base of the geographically distinct food web (McClelland & Montoya 2002; McMahon et al. 2010; Boecklen et al. 2011). In contrast, trophic or non-essential amino acids such as glutamic acid greatly enrich in $\delta^{15}N$ during each trophic step (McClelland & Montoya 2002; Ohkouchi et al. 2017). By modelling the differential fractionation between these essential and non-essential amino acids, a consumer's trophic position can be estimated in relation to a known food web (across temporal and spatial scales) (Ohkouchi et al. 2017). This area of research is rapidly moving forward through multi-investigative approaches, including laboratory diet feeding trials, estimating baseline isotopic values for terrestrial and aquatic environments, accurately investigating the source and trophic amino acid pairing, and through the application of tracking technology (McMahon et al. 2010; Steffan et al. 2013; Ohkouchi et al. 2017; Polito et al. 2017), but discrepancies and variability still needs to be addressed.

Study Species

Distribution and abundance

The Hutton's shearwater is a small black and white shearwater that was first described by Mathews in 1912 (Falla 1965; Marchant & Higgins 1990). Hutton's shearwaters (*Puffinus huttoni*) are classified as "endangered" (IUCN Red List) and "threatened and nationally vulnerable" under the New Zealand Threat Classification (Birdlife International 2017; Robertson et al. 2017). They are alpine-breeding birds (Worthy & Holdaway 1995), nesting solely in the Seaward Kaikōura Ranges or more recently within a predator-proof colony on the Kaikōura Peninsula (see below) (Rowe 2014). Up until 1965, the breeding location of Hutton's shearwater was unknown although they were observed at sea rafting within coastal areas near Kaikōura (Harrow 1965, 1976). From a conversation with locals hunters reporting 'muttonbirds' or 'titi' nesting in the mountains, Geoff Harrow investigated the alleged location of these birds (Harrow 1965). Over several years, eight breeding colonies were identified within the Seaward and Inland Kaikōura Ranges, all above 1200 m.a.s.l (Harrow 1976; Sherley 1992). Unfortunately, by the 1980's these colonies had been reduced to just two areas (Kaikōura River and Shearwater Stream), predominantly due to mammalian predation (especially feral pigs *Sus scrofa*) (Cuthbert 2002; Sommer et al. 2009). The estimated Kowhai River colony population in the 1980's was approximately 134,000 used burrows (Sherley 1992), but this estimate was reassessed in 2007–08 to around 106,000 breeding pairs for the Kowhai River colony and an estimate of 8000 pairs in the Shearwater Stream colony (Sommer et al. 2009).

Breeding ecology

Hutton's shearwaters are absent from New Zealand waters during the non-breeding period and are reported to circumnavigate Australia (Marchant & Higgins 1990). At the start of the breeding season, adult birds start returning to New Zealand during late August (Harrow 1976; Cuthbert 2001). The alpine burrows are located amongst bluffs and shingle screes and are generally covered in thick snow on first arrival (Harrow 1976; Cuthbert & Davis 2002). Birds visit the colony at night and remain sitting on the snow surface until the area clears; during the day birds head to sea. Males defend their burrow from other conspecifics. During mid-October, birds depart on a pre-laying exodus (Harrow 1976). A single egg is laid by each breeding pair from late October to late November. Incubation lasts on average 50.3 ± 2.0 days, and chicks start fledging late March-early April after approximately 83.8 days (Cuthbert 2001). If the egg is unsuccessful, shearwaters will not lay a replacement egg (Warham 1990). Chicks hatch with a natal down and will produce a secondary down before growing juvenile plumage (Harrow 1976; Marchant & Higgins 1990). Both adults feed the chick for approximately two months. Once the chicks leave the colony, they remain at sea until they reach the age of three-four years, before returning to their natal colony (Marchant & Higgins 1990; Cuthbert 2001).

Foraging behaviour

Little is known of the foraging behaviour of the Hutton's shearwater, but through observed rafting behaviour in the near Kaikōura region (Harrow 1976), it is believed that this is a main foraging area. The diet of the Hutton's shearwater has not been investigated in detail, but the current literature indicates it includes fish, crustacean and squid (Harrow 1976; Tarburton 1981; West & Imber 1985). Hutton's shearwaters

have been observed feeding on small unidentified shoaling fish off the Kaikōura coast, and rafting near Gore Bay, off Banks Peninsula and at the entrance of Cook Strait (Harrow 1976). Two by-catch events have been reported where Hutton's shearwaters were found drowned in fishing nets off the Kaikōura Peninsula (Tarburton 1981; West & Imber 1985). Stomach content analysis identified crustaceans, squid beaks and thin 'fingerling' fish; two fish tentatively identified as a small pelagic clupeid (*Sprattus antipodarium*) and larval wrasse (*Pseudolabrus* sp.).

Perhaps to reduce inter- and intra-species competition, seabirds will travel varying distances from their breeding colony to forage (Kojadinovic et al. 2008b; Jaeger et al. 2010). It is uncertain what mechanisms influence Hutton's shearwater foraging behaviour, but observations have identified individuals foraging with conspecifics as well as with red-billed gulls (*Larus novaehollandiae*), black-backed gulls (*Larus dominicanus*), white-fronted terns (*Sterna striata*) and Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand, and wedge-tailed shearwater (*Puffinus pacificus*) in Western Australia (Harrow 1976; Halse 1981; Marchant & Higgins 1990; Brager 1998). With the variability in foraging style, diving depths and prey preference, niche segregation may occur between these species (Navarro et al. 2013).

Sexual segregation has been identified in other procellariiform species (e.g., wedge-tailed shearwater and southern giant petrel *Macronectes giganteus*) during the chick-rearing period (Forero et al. 2005; Peck & Congdon 2006) and this may also be the case in Hutton's shearwater. This species has been seen to form large rafts of foraging birds, but the age structure or experience of birds in these flocks are unknown (Harrow 1976; Marchant & Higgins 1990). Immature individuals may be excluded

from these foraging flocks, not through aggressive behaviour but competitive exclusion (Fayet et al. 2015). It has been proposed that the spatial segregation seen in Manx shearwater is largely due to the lack of skill in immature birds to capture food and being outcompeted by the adults (Fayet et al. 2015). This pressure on hunting ability may lead to spatio-temporal segregation and foraging in the less productive areas maybe more beneficial.

Conservation

Predation by introduced mammals is a major cause of decline in seabirds around the world, including New Zealand, and the impacts of predators on the Hutton's shearwater (Cuthbert 2001). For the two surviving alpine colonies, the high altitude and remoteness does confer a form of protection, but the presence of stoats (*Mustela erminea*), feral cats (*Felis catus*) and feral pigs (*Sos scrofa*) pose the highest risk (Cuthbert 2001, 2002, 2003). Although feral pigs have been implicated as the main cause of the loss of the six extirpated colonies, some evidence has been found of pigs, red deer (*Cervus elaphus*) and goats (*Capra hircus*) within the extant alpine colonies despite the steep terrain (Cuthbert 2001; Cuthbert & Sommer 2009). Unfortunately, this isolation and restricted access could be dramatically changed through land movement (e.g., erosion) (Cuthbert 2001). Cuthbert (2002) found that controlling stoat predation through trapping over two breeding seasons resulted in no measurable increase in breeding success within the alpine birds as predicted. Alternatively, three native predators may also affect breeding success and chick survival; these are Australasian harrier (*Circus approximans*), New Zealand falcon (*Falco novaezeelandicae*) and kea (*Nestor notabilis*) (Harrow 1976; Cuthbert 2003). It has

been proposed that at sea or other environmental factors may be more important in population regulation than predation at the two surviving colonies (Cuthbert 2002).

To aid in population recovery and to safeguard against future losses, the Department of Conservation (DOC) and Whale Watch Kaikōura established a third colony. In 2005, suitable land was identified on the Kaikōura Peninsula and after an initial trial transfer of 10 individuals; approximately 100 nestlings were translocated from the alpine colony to the peninsula site each year during March (2006–08). In 2008, the Hutton's Shearwater Charitable Trust was established and fundraising for a predator-proof fence was undertaken, and installation was completed by February 2010 (Rowe 2014). During 2012 and 2013, a further ~200 nestlings were introduced to the peninsula colony. The one-hectare fenced site contains artificial burrows (nesting boxes) and to aid the colony establishment process and chick homing ability, each chick was hand-feed over each translocation season (Miskelly et al. 2009). Of the ~500 birds that have been translocated over 65 individuals have returned to the colony and ~15 pairs are currently breeding (Rowe *pers. comm*). From a group of translocated individuals, one breeding pair has been successful in producing a third generation chick at the Kaikōura Peninsula colony.

To conserve a species, three priority areas need to be addressed: 1) predator eradication and control of invasive alien species, 2) habitat restoration and protection (on land and at sea), and 3) foraging locations and mitigation of seabird by-catch (Croxall et al. 2012). As terrestrial areas are generally easier to access and assess, land-based protection areas are not surprisingly better protected through regulation and management strategies. Similarly, predator control and the reduction of invasive

species are becoming normal practice in conservation management planning on mainland areas and islands (Croxall et al. 2012). However, a fuller understanding of the foraging locations, dietary choice, and potential threats at sea including fisheries (competition or by-catch), climate change, and anthropogenic impacts (e.g., oil spills, wind farms, shipping lanes) is lacking for many species, including Hutton's shearwater (Piatt et al. 1990; Croxall et al. 2012; Spiegel et al. 2017). To further understand the conservation and management of this species, research into its diet, foraging areas, and ecology needs to be undertaken (Cuthbert 2001). My aim is to fill some of the gaps in our knowledge of the at sea behaviour and ecology of Hutton's shearwater, in order to aid its conservation in the long-term.

Objectives

In this thesis, I had four objectives:

1. To assess the diving behaviour of Hutton's shearwater during the breeding period using Time-Depth Recorders (TDRs)
2. To investigate dietary differences between the breeding and non-breeding periods and sexes using Stable Isotope Analyses (SIA)
3. To track adults using GPS to identify foraging locations during the chick-rearing period
4. To use SIA to infer the maternal contribution and the progressive formation of chick feathers compared to adult diet and feather

These objectives will be addressed using a multidisciplinary approach and a variety of research methods.

General Methodology

The research in this thesis adds to the increasing literature that uses bio-logging devices and stable isotope ratio analysis to study the behaviour of marine organisms and how a species responds to environmental conditions (Burger & Shaffer 2008; Bond & Jones 2009; Latham et al. 2015). Specifically, Global Positioning System (GPS) devices and Time-Depth Recorders (TDRs) were used to track the foraging activities of Hutton's shearwater adults during the breeding season. The TDR units recorded dive depth and duration every five seconds, whereas the GPS units (PinPoint50 and Uria100) recorded the birds' location at varying frequencies (5–60 minutes); Uria100 units also recorded dive duration. Loggers were deployed on adult breeding birds from the Kaikōura Peninsula colony, during the 2014–15 breeding season (TDRs) and 2017 chick-rearing period (TDRs and GPS). Stable isotope analysis (SIA) was used to investigate the diet and trophic relationships, and to gain an insight into the foraging ecology of the Hutton's shearwater (Inger & Bearhop 2008). Feather samples were collected from breeding adults and chicks from the alpine Kowhai Stream and the Kaikōura Peninsula colonies, during the 2014–15 breeding season.

Studying foraging behaviour using different types of loggers and through stable isotope analysis allows a range of questions to be asked. The combination of these techniques will increase our knowledge of the Hutton's shearwater and provide a baseline for future conservation efforts.

Outline of thesis

The thesis is structured in manuscript form with the central chapters reporting on specific studies that will be prepared for publication. The overall goal was to study the Hutton's shearwater in a wider ecosystem context by identifying diving behaviour, diet and habitat preferences. Chapter 2 examines the depth, duration and frequency of diving by breeding adults through the deployment of Time-Depth Recorders (TDRs). Chapter 3 investigates the diet and sexual segregation of adults during the breeding and non-breeding period. Chapter 4 combines data from GPS and TDR devices (2017) to identify locations that breeding adults visit and potentially forage in, to provision themselves and to feed their chicks. Chapter 5 attempts to link the endogenous isotopic composition of the resources stored by breeding females during the pre-breeding period and the utilisation of these nutrients in the formation of the egg. I also aim to assess the transition from maternal nutrient composition to the adult provisioning/supplied (endogenous) and similarity to adult feather composition. Adult and chick feathers will be used as proxies for each transitional stage. Chapter 6 will provide a review of these chapters, and highlight areas for which further research is needed.

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Hutton's shearwater adult equipped with a Time-Depth Recorder, 24 January 2015 (Photo by SW Marriott).

Chapter 2

Variation in diving behaviour of Hutton's shearwater (*Puffinus huttoni*)

Abstract

With the development and implementation of tracking technology, we are now able to monitor the foraging behaviour of seabirds while at sea. Time-Depth Recorders (TDRs) were fitted to Hutton's shearwaters (*Puffinus huttoni*), an endangered species endemic to New Zealand, to measure diving behaviour and to compare it between incubation and chick-rearing periods. I found Hutton's shearwaters dive up to 339 times per day (average 68.8) at depths to 35 m (average 5.6 m), and for periods up to 60 s (average 19.2 s). Dives were shallower but of longer duration than expected from other Procellariiforme species. Incubating birds dived deeper than birds feeding chicks, and a significant difference in diving depth and dive duration was detected at different times of the day. The temporal and seasonal variation I observed in the diving behaviour of Hutton's shearwaters suggests they are likely to exploit different types of pelagic prey at different stages in their breeding cycle. With on-going changes in the marine environment, monitoring changes in feeding behaviour using TDRs may provide a way to assess environmental change and improve the conservation of this species.

Introduction

Seabirds are top predators within many marine ecosystems, and they are important in maintaining oceanic food webs (Shaffer et al. 2006; Neves et al. 2012). Species in the Procellariiformes and Sphenisciformes, in particular, are the most pelagic of all seabirds, with many foraging over great distances and for extended periods of time at sea (Barlow & Croxall 2002; Shaffer et al. 2006; González-Solís et al. 2007; Carpenter-Kling et al. 2017). As a consequence, it has been suggested that studies of Procellariiformes provide a valuable indicator of marine environmental change and health (Neves et al. 2012). However, tracking movements and foraging behaviours of pelagic birds can be difficult as individuals spend extended periods of time at sea. Thus, there are gaps in our knowledge with regards to their patterns of migration, dispersal, moult, and foraging behaviour (West & Imber 1985; Warham 1996; Ropert-Coudert & Wilson 2005). With the development of tracking devices that allow us to follow and monitor individual birds, we are now more able to study their behaviour while at sea.

Some seabird species use different marine habitats depending on the stage of their breeding cycle and the energetic costs to reach these areas. For example, longer foraging trips away from the breeding colony have been attributed to self-maintenance, whereas shorter trips are mainly used for chick provisioning (Paiva et al. 2010a). Such bimodal foraging strategies have been observed during the breeding season in several species (Weimerskirch & Cherel 1998; Shoji et al. 2015). Habitat heterogeneity can also influence diving behaviour as it requires a degree of plasticity in foraging behaviours to exploit the patchiness and variability of available prey (Shaffer et al. 2009; Paiva et al. 2010b; Dias et al. 2011). Likewise, diving depths are

known to be influenced by environmental conditions, including changes in bathymetry, wind direction and upwelling (Raymond et al. 2010; Cleeland et al. 2014; Meier et al. 2015). Paiva et al. (2010a) found shorter and shallower dives occurred in Cory's shearwater (*Calonectris borealis*) within coastal upwelling areas compared to the longer and deeper dives within oceanic waters. However, not all seabird species exhibit this variation, as diving depths in the sooty shearwater (*Puffinus grisea*) were not significantly different between short and long foraging trips (Shaffer et al. 2009). For most shearwater species, there is a lack of data to determine how diving behaviour varies with the breeding season and environmental conditions.

Shearwaters of the genus *Puffinus* forage by a combination of pursuit diving, plunging or surface seizure. Sooty, flesh-footed (*Puffinus carneipes*) and fluttering (*Puffinus gavia*) shearwaters search for prey by lowering their heads below the surface before submerging and chasing potential prey (Warham 1990). Nevertheless, the parameters associated with diving behaviour, in which birds actively swim to depth to pursue prey, appears to vary among species. By using Time-Depth Recorders (TDR) fitted to Sooty shearwaters, Dunphy et al. (2015) recorded maximum dive depths of 55.1 m. In contrast, maximum depth of grey-faced petrels (*Pterodroma gouldi*) and streaked shearwater (*Calonectris leucomelas)*, reached only 2.41 m and 6.0 m, respectively (Matsumoto et al. 2012; Dunphy et al. 2015). Although maximum diving depths are known for some Procellariiforms (Taylor 2008), detailed estimates of diving behaviour are lacking in most species. It is still not fully known how diving behaviour in terms of depths, frequency and duration varies within a species, such as might occur at different stages in the breeding cycle (e.g., incubating *vs*. chick provisioning), or times of day (e.g., in response to diurnal cycles in the distribution and availability

of their prey) (Alonso et al. 2014; Jaeger et al. 2014; Elliott & Gaston 2015; Campioni et al. 2016). By assessing the various diving depths and diving durations used to acquire food resources over the breeding season, these behaviours can be used as indicators of environmental change and to adapt conservation strategies (Ropert-Coudert & Wilson 2005; Shaffer et al. 2006; Grémillet et al. 2014; Meier et al. 2015).

The Hutton's shearwater is an endemic and endangered seabird breeding only in the Seaward Kaikōura Ranges (Harrow 1965), and more recently on the Kaikōura Peninsula (Te Rae o Atiu). The marine environment in this area is subject to increasing pressure from fisheries, tourism and deep-sea oil exploration (Tarburton 1981; Uruski 2010; Markowitz et al. 2011; Velando & Munilla 2011; Rollinson et al. 2014). Little is known about the foraging behaviour of this species nor how it may be affected by changes in the marine environment. The objectives of this study were to: (1) describe the diving behaviour of Hutton's shearwater while they are at sea through the deployment of miniaturised TDR's, and (2) to determine how diving behaviour varies temporally, both across the breeding cycle and over the course of the day. I compared dive depth, dive duration, and the number of dives between shearwaters that were incubating eggs vs. those feeding chicks. I also compared my observations of Hutton's shearwaters with that of the diving depths and duration expected from studies across other shearwater species. My data provides a baseline for future studies to determine how this species might cope with ongoing environmental changes.

Methods

Time-Depth Recorder deployment

The diving behaviour of the Hutton's shearwater was studied by deploying TDR loggers on incubating adult birds during the 2014/15 breeding season. LAT1500 TDR loggers (8 × 32 mm, 3.4 g, 512 Kb memory, Lotek Wireless) were used on eight Hutton's shearwater adults breeding in the Te Rae o Atiu colony on the Kaikōura Peninsula (42°25'42.72"S, 173°42'10.54"E; Figure 2.1). The colony currently contains 16 pairs of breeding Hutton's shearwater. Only one breeding adult was chosen from each nesting pair with four males and four females selected (sex confirmed by DNA testing). Six breeding pairs were successful in fledging a chick whereas two pairs failed during incubation (only 1 egg is laid per clutch). Only the successful breeders were used during analysis. All birds had been banded previously and were aged between seven to nine years at the time of the study, and in their third to fifth breeding season.

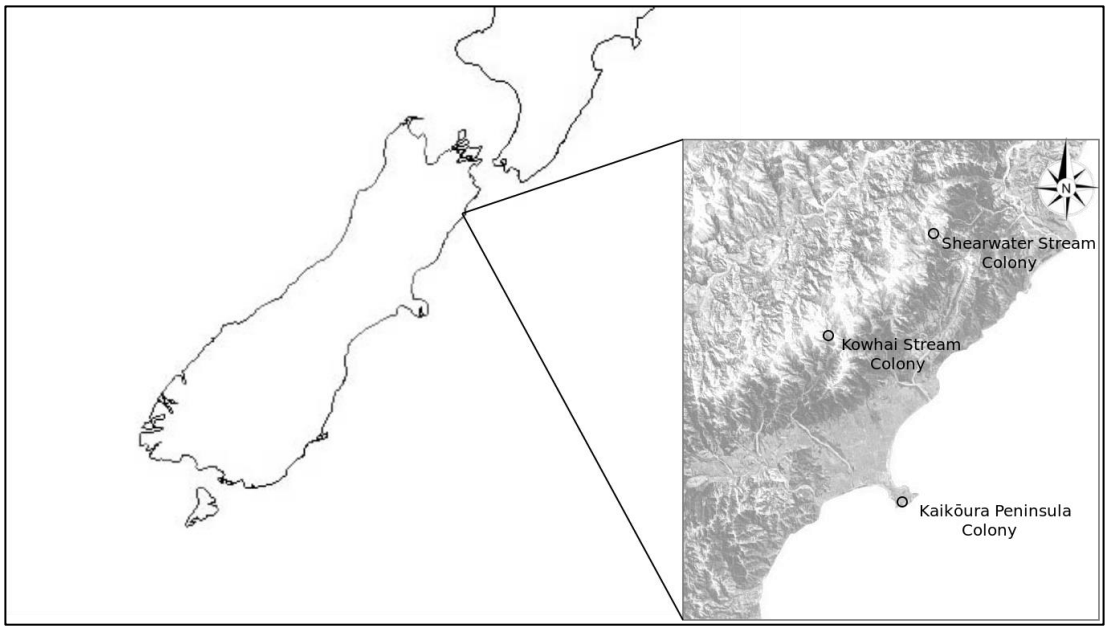

Figure 2.1 Map of the South Island with the insert showing the natural breeding sites in the Seaward Kaikōura Ranges and the coastal Kaikōura Peninsula colony (Te Rai o Atiu). TDR loggers were deployed on adult breeding birds from the Kaikōura Peninsula colony.

To fit the TDR loggers, birds were caught by hand from within the artificial nesting boxes provided in the colony and held within a black cotton bag to reduce stress and prevent biting. TDR loggers were attached to E-sized plastic leg bands using cable ties with steel locking barb and epoxy Araldite glue. These bands were attached to the left tarsometatarus of the adult, and secured with a second cable tie and super glue to prevent the logger being removed while going in and out of the burrow. TDR loggers were secured with the pressure sensor facing towards the foot to limit potential effects of acceleration (Elliott et al. 2008). Combined weight and attachment (4.5 g, 1.28 %) of each logger was within 3 % of a bird's body weight (~350 g; Warham 1977; Cuthbert 2001). Logger deployments were completed between 10:00–14:30 h. After fitting the TDRs, birds had to be recaptured to recover and download each logger. All recaptures and retrievals of TDR loggers were carried out at night from 00:30–03:00 h. When birds arrived back at the colony, time was allowed for adults to provision

chicks, to prevent food loss due to human disturbance. The time taken to capture birds, and attach or retrieve the loggers took less than ten minutes. All birds were released back into their burrows. Immediately after release, the burrow end was covered for a few minutes allowing the bird to resettle on the egg or with the chick. Dive depth analysis was set to 'when wet and ≥1.5 m' to remove TDR manufacturing error (1 % error over 100 m = 1.0 m error) and barometric pressure influence on the top 0.5 m of water. During each capture, birds were examined to assess any signs of distress or skin damage caused by the TDR units; none was recorded.

The TDR loggers recorded pressure (resolution 0.05%) and internal device temperature (resolution $>0.05^0$ C), and wet/dry state at 5-second intervals. TDR loggers were deployed from 24–25 November 2014 to 22–24 January 2015 (11–36 logged days), and recorded 222 foraging trips (14,644 diving records). Data was recovered from six TDR loggers. Recapture of individual birds took between 2 and 16 days. One logger stopped working part way through the deployment period. No nest abandonment, egg damage or chick loss occurred.

Data analysis

All data files were downloaded (Lotek, Tag Talk, Canada) and processed through the program MultiTrace-Dive (Jensen Software Systems, Germany; version 2014.5.0.0).

To examine whether diving behaviour changed over the breeding season, the data set was divided into incubation and chick-rearing periods, and subsequently sub-divided into early incubation and chick-rearing and late incubation and chick-rearing stages. These subdivided periods were determined by aligning hatch dates and dividing the

pre-hatch data collection period into early incubation (days 1–14 after laying) and late incubation (days 15–28 after laying), and the post-hatch period into early chick-rearing (days 1–18 after hatch) and late chick-rearing (days 19–36 after hatch). Status (incubation or chick-rearing), period (early incubation, late incubation, early chick-rearing and late chick-rearing) and time (grouped hourly) effects on diving depth and dive duration values were estimated in a linear mixed-effects model framework (R package *lme4*, version 1.1–7, Bates et al. 2015) with dive depth and dive duration data logarithmic transformed using R version 3.3.0 (R Core Team 2017). The effects of individual identification ("bird") and date were included as random effects on the intercept, taking the correlation between repeated measurements on the same individuals into account. Model selection was performed using the Akaike's Information Criterion corrected for finite sample size (AIC_c) (Hurvich & Tsai 1989) to determine the best model (R package *boot*, version 1.3–18). A model was identified as the best model when it had the lowest AIC_c value with a difference >2 compared with the second best model (Table 2.1). I used a parametric bootstrap to estimate the confidence intervals (R package MuMIn, version 1.15.6). Test significance was assessed by checking whether the confidence intervals at a particular alpha-level include zero. Negative and positive values showed the direction of the statistical difference. Unless otherwise stated, all values are presented as mean ± predicted 95% confidence intervals.

To compare the diving depths of Hutton's shearwater to other Procellariforms, I applied Burger's (1991) allometric equation, which was originally modelled to examine the diving depths of penguins and alcids: $D_{max} = 75.905\ M^{0.316}$, where D is maximum dive depth, and M is mass in kg (Burger 1991). To compare dive duration,

I used the allometric equation from Halsey et al. (2006b): $D_{duration} = 35.5\ M^{0.326}$, where D is the average maximum dive duration and M is mass in kg. This equation was modelled taking 195 species from 286 studies into account (Halsey et al. 2006b). Each equation was computed using the average body mass measurements and diving behaviour reported by other publications.

Results

Hutton's shearwaters dived almost exclusively during the daylight hours. From the recorded dives, only 12 dive events (<0.07 %; *n* = 14,632) occurred between 22:00 and 04:00 h (mean dive depth: 5.96 m ± 2.08, range 1.58–10.38 m). These events were recorded within the hour following 02:00 h (female, *n* = 1), 04:00 h (male, *n* = 2), and 22:00 h (male, *n* = 6 and female, *n* = 3), and represent 0.07 % of the overall diving activity. Only four of the 12 night dives occurred within 72 hours of a full moon. These events were classed as 'night dives,' and because of the small sample size, they were removed from the remaining data set.

Diving depth

The maximum dive depth recorded for all sampled birds was 35.0 m (female); the maximum dive depth for a male was 32.2 m. The average maximum dive depth (mean maximum depth per day) for all birds was 15.0 m (CI = 0.92 m, *n* = 216 days). The average daily diving depth was 5.6 m (CI = 0.08 m, *n* = 14,632 dives) for all birds and 5.3 m (CI = 0.08 m, *n* = 13,137) for only those birds that were successful breeders.

For the successful breeding birds, average dive depths differed between the incubation (6.6 m ± 0.16, *n* = 5068 dives) and chick-rearing periods (4.5 m ± 0.08, *n* = 8069 dives), and differences in the average diving depth were also detected between the early (7.5 m ± 0.21, *n* = 3691 dives) and late incubation periods (4.1 m ± 0.19, *n* = 1377 dives), and the early (4.7 m ± 0.09, *n* = 5741 dives) and late chick-rearing periods (4.2 m ± 0.13, *n* = 2328 dives). Significant differences were detected in average diving depths between each breeding period (Table 2.1). The difference in dive depth between the different periods was significant between the early chick-rearing (intercept; Std. Est. 3.60, [CI 3.05, 4.25]), late chick-rearing (Std. Est. 0.92, [CI 0.88, 0.95]) and early incubation (Std. Est. 1.48, [CI 1.44, 1.53]), but not significant between the early chick-rearing and late incubation periods (Std. Est. 0.98, [CI 0.94, 1.02]). A significant difference in diving depth was also found between the early chick-rearing, early and late incubation periods when date was taken into account (intercept; Std. Est. 3.64, [CI 3.09, 4.29], Std. Est. 1.31, [CI 1.20, 1.43]; Std. Est. 1.08, [CI 1.02, 1.14], respectively), but no difference was observed in the late chick-rearing period (Std. Est. 0.99, [CI 0.94, 1.03]; Table 2.1).

Table 2.1 Comparison of linear mixed-effects models to explain depth and duration of dives. Selected models are in bold. 'Bird' was used as a random variable for all models unless otherwise stated. 'Status' includes incubation or chick-rearing periods. 'Period' comprises early and late incubation and early and late chick-rearing periods. 'BinTime' incorporates dives recorded within an hour into a single data set by hour. Log likelihood = natural logarithm of the maximum likelihood for the model; AICc = Akaike Information Criterion model score; ΔAICc = difference in Akaike Information Criterion score between models; Weight = Akaike Information Criterion weights.

Model	d.f.	Log Likelihood	AICc	ΔAICc	Weight (w_i)
Dive depth					
Null	3	–13,856.16	27,718.32	883.54	1.39E–192
Status	4	–13,599.42	27,206.84	372.06	1.62E–81
Period	**6**	**–13,411.39**	**26,834.78**	**0.00**	**1.00E+00**
Dive duration					
Null	3	–8366.08	16,738.15	505.11	2.70E–110
Status	4	–8244.15	16,496.31	263.27	6.79E–58
Period	**6**	**–8110.52**	**16,233.04**	**0.00**	**1.00E+00**
Ave. number of dives per hour					
Null	3	–467.43	940.95	5.69	5.47E–02
Status*Time	**36**	**–426.68**	**935.25**	**0.00**	**9.44E–01**
Period*Time	70	–382.92	948.14	12.89	1.50E–03
Dive depth with Time					
Null	3	–13,856.16	27,718.32	1503.28	0.00E+00
BinTime	19	–13,652.00	27,342.05	1127.01	1.87E–245
Status	4	–13,599.42	27,206.84	991.8	4.30E–216
Period	6	–13,411.39	26,834.78	619.74	2.66E–135
Status + BinTime	20	–13,407.77	26,855.60	640.56	8.02E–140
Status + BinTime + Status*BinTime	36	–13,345.36	26,762.92	547.88	1.07E–119
Period + BinTime	22	–13,223.96	26,492.00	276.96	7.23E–61
Period + BinTime + Period*BinTime	**70**	**–13,037.14**	**26,215.04**	**0.00**	**1.00E+00**
Duration with Time					
Null	3	–8366.08	16,738.15	982.11	5.46E–214
Status	4	–8244.15	16,496.31	740.27	1.79E–161
BinTime	19	–8168.38	16,374.81	618.77	4.32E–135
Period	6	–8110.52	16,233.04	477	2.63E–104
Status + BinTime	20	–8072.63	16,185.31	429.27	6.10E–94
Status + BinTime + Status*BinTime	36	–8008.18	16,088.56	332.52	6.23E–73
Period + BinTime	22	–7953.86	15,951.79	195.75	3.11E–43
Period + BinTime + Period*BinTime	**70**	**–7807.64**	**15,756.04**	**0.00**	**1.00E+00**
Dive depth with Date					
Null (1|Bird) + (1|Date)	4	–12,613.64	25,235.28	16.17	3.05E–04
Status + (1|Bird)	4	–13,599.42	27,206.84	1987.73	0.00E+00
Status + (1|Date)	4	–12,777.65	25,563.29	344.18	1.81E–75

Status + (1|Bird) + (1|Date)	5	–12,609.22	25,228.44	9.33	9.33E–03
Period + (1|Bird)	6	–13,411.39	26,834.78	1615.67	0.00E+00
Period + (1|Date)	6	–12,782.92	25,577.84	358.73	1.25E–78
Period + (1|Bird) + (1|Date)	**7**	**–12,602.55**	**25,219.11**	**0.00**	**9.90E–01**
Duration with Date					
Null (1|Bird) + (1|Date)	4	–7441.61	14,891.23	-7.81	9.80E–01
Status + (1|Bird)	4	–8244.15	16,496.31	1597.27	0.00E+00
Status + (1|Date)	4	–7471.81	14,951.63	52.59	7.51E–14
Status + (1|Bird) + (1|Date)	**5**	**–7444.52**	**14,899.04**	**0.00**	**1.97E–02**
Period + (1|Bird)	6	–8110.52	16,233.04	1334	4.18E–292
Period + (1|Date)	6	–7475.08	14,962.16	63.12	3.88E–16
Period + (1|Bird) + (1|Date)	7	–7450.34	14,914.70	15.66	7.85E–06
Ave. number of dives per hour with Date					
Null (Bird + Date)	**4**	**–2220.39**	**4448.8**	**0.00**	**1.69E–03**
Status*Time + (1|Bird)	36	–2230.64	4535.11	86.31	3.06E–22
Status*Time + (1|Date)	36	–2230.33	4534.48	85.68	4.19E–22
Status*Time + (1|Bird) + (1|Date)	37	–2224.37	4524.67	75.87	5.65E–20
Period*Time + (1|Bird)	70	–2209.25	4565.49	116.69	7.72E–29
Period*Time + (1|Date)	70	–2210.46	4567.92	119.12	2.30E–29
Period*Time + (1|Bird) + (1|Date)	71	–2204.34	4557.87	109.07	3.50E–27

Significant differences in breeding period by time of day interactions were found for diving depths per hour (Table 2.1; Figure 2.2). Dives tended to be deeper in the early morning (05:00–7:00 h) and mid-afternoon (13:00–18:00 h) in both the early and late incubation period (Appendix 1). Few deep dives were observed during the middle of the day (09:00–16:00 h). By the chick-rearing period, dive depths were shallow throughout the day, but an increase in depths was observed in the early morning (05:00–07:00 h), mid-afternoon (14:00–17:00 h) and late evening (20:00–21:00 h).

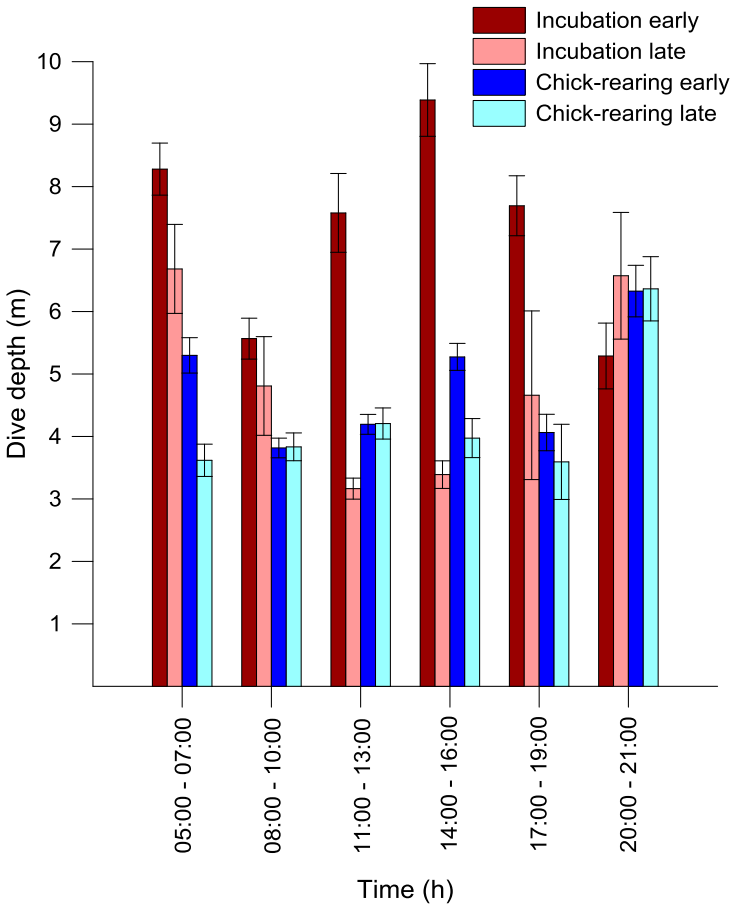

Figure 2.2 Hutton's shearwater diving depth assessed by time of day (h) during the incubation and chick-rearing period (2014–15). Average dive depth (m) performed per hour (± CI) are shown during the early and late incubation and chick-rearing periods.

Diving frequency

An average of 68.8 dives (CI = 8.22, *n* = 191 days) were recorded per individual per day (range 1–339 dives/day). The total number of dives recorded over a period of 11–36 TDR logging days ranged from 1749 to 2641 dives per individual. A decrease in the daily rate of diving frequency was observed between the early incubation (102.5 ± 23.9 dives/day, *n* = 36 days) and late incubation (59.9 ± 25.7 dives/day, *n* = 23 days). This was followed by an increase in diving frequency during the early chick-rearing period (70.0 ± 10.6 dives/day, *n* = 82 days) before it declined again in late chick-rearing (46.6 ± 14.1 dives/day, *n* = 50 days). A significant difference in the number of

dives per day was detected between the early (intercept; Std. Est. 39.89, [CI 31.23, 50.90]) and late chick-rearing, and early and late incubation periods (Std. Est. 0.62, [CI 0.44, 0.87]; Std. Est. 0.638, [CI 0.48, 0.86]; Std. Est. 0.40, [CI 0.28, 0.59], respectively). However, when dive frequency with date was analysed, the null model best explained the data indicating that date had no effect on dive frequency independent of the chick-rearing and incubation periods (Table 2.1).

A significant status (incubation and chick-rearing) by time interaction was found for the average number of dives per hour (Std. Est. –0.42, [CI –1.28, 0.43]; intercept; Std. Est. 3.85, [CI 3.24, 4.46], respectively; Table 2.1). Significant differences were detected between the incubation period at 19:00 h (Figure 2.3; Std. Est. 3.71 [CI 1.04, 13.10]; Appendix 3) and chick-rearing at 10:00 h (intercept; Std. Est. 47.00, [CI 25.65, 86.09]), and within the chick-rearing period at 5:00 h (Std. Est. 0.15, [CI 0.06, 0.43]) and between 18:00–20:00 h (Std. Est. 0.27, [CI 0.12, 0.63]; Std. Est. 0.20, [CI 0.08, 0.48]; Std. Est. 0.196, [CI 0.083, 0.461], respectively).

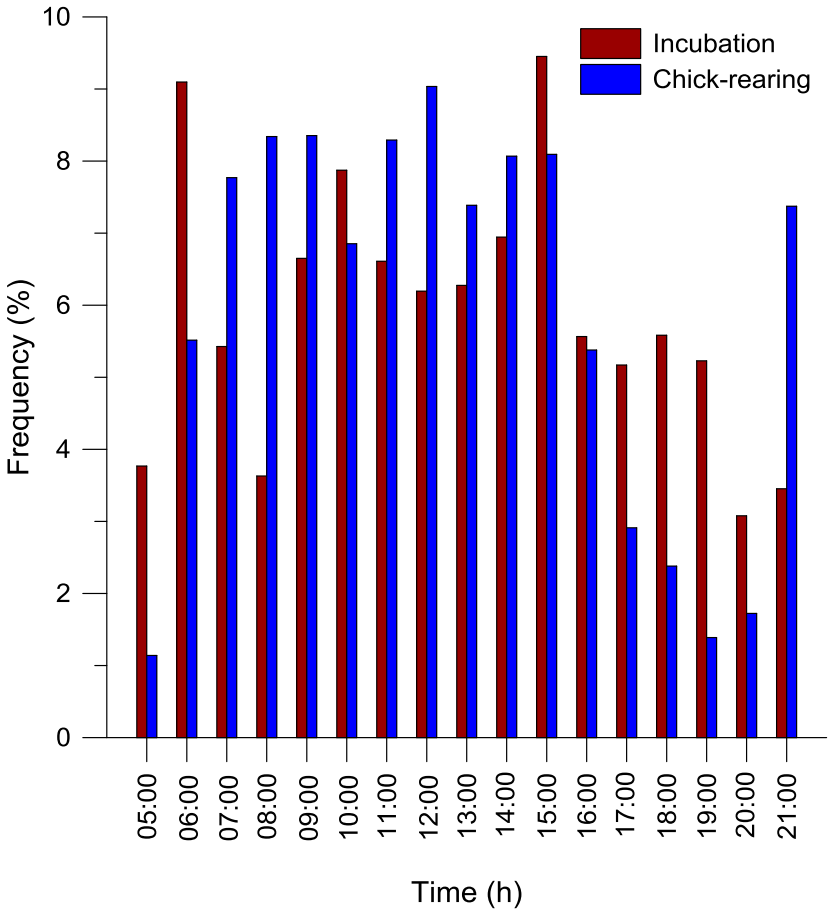

Figure 2.3 Frequency of dives (%) by Hutton's shearwaters in relation to time of day (h) during the incubation (n = 5068 dives) and chick-rearing period (n = 8069 dives).

Dive duration

The maximum and average maximum dive durations recorded were 67.5 and 35.7 ± 1.68 s (n = 191; deepest dive record per day for each bird), respectively. The average diving duration was 19.2 ± 0.17 s (n = 13,137 dives; range = 5.0–67.5 s). There was a significant difference between the average dive durations during the incubation (21.1 ± 0.33 s, n = 5068 dives) and chick-rearing periods (18.0 ± 0.17 s, n = 8069 dives).

Significant differences were also detected in diving duration between each breeding period (Table 2.1). A significant difference was found between the early (22.8 ± 0.42

s, *n* = 3691 dives) and late (16.3 ± 0.39 s, *n* = 1377 dives) incubation, and early (18.2 ± 0.21 s, *n* = 5741 dives) and late chick-rearing periods (17.6 ± 0.32 s, *n* = 2328 dives) (early chick-rearing: (intercept) Std. Est. 16.36, [CI 15.21, 17.60]; late chick-rearing: Std. Est. 0.96, [CI 0.94, 0.99]; early incubation: Std. Est. 1.21, [CI 1.19, 1.24]; late incubation: Std. Est. 0.95, [CI 0.93, 0.98]). A significant difference in breeding period by time interaction was found for diving duration per hour (Table 2.1). Time of day had a significant effect on dive duration throughout the daylight hours (Figure 2.4; Appendix 2). Dive durations were longest in the early mornings and afternoons, especially during the early incubation period. However, no significant difference was observed between the chick-rearing and incubation periods for dive duration when date was taken into account (intercept) Std. Est. 16.66, [CI 15.50, 17.89]; Std. Est. 0.99, [CI 0.95, 1.02], respectively; Table 2.1).

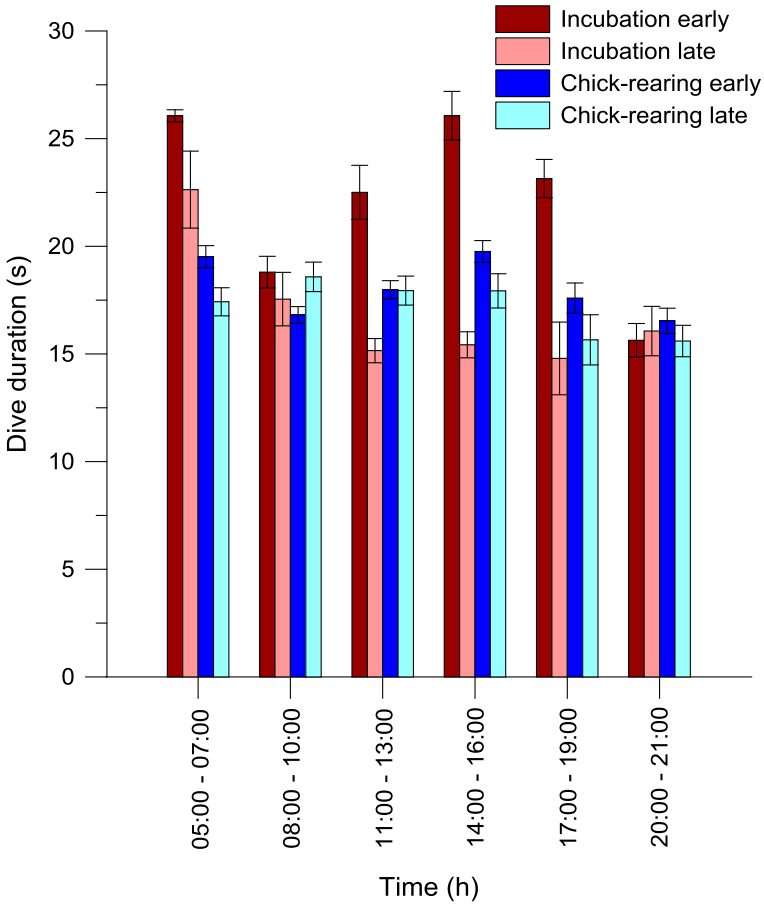

Figure 2.4 Hutton's shearwater dive duration assessed by time of day (h) during the incubation and chick-rearing period (2014–15). Average dive duration (s) performed per hour (± CI) are shown during the early and late incubation and chick-rearing periods.

Allometric analysis

Calculated maximum dive depth and dive duration for other Procellariiforms are reported in Table 2.2. The expected maximum dive depth and average maximum dive duration for Hutton's shearwater were calculated to be 54.5 m and 25.2 s, respectively (Table 2.2). This is greater than the maximum dive depth recorded (35.0 m), but the observed dive durations (35.7 s) were about a third longer than expected. Thus, Hutton's shearwaters have shallower dives but dived for longer periods per dive than expected when compared to other Procellariiforms.

Table 2.2 Summary of Time-Depth Recorder (TDR) data from shearwater species from the literature. For each species, the sample size, body mass, dive depth and duration of dives is presented. Scientific names in accordance to the IOC World List (Gill & Donsker 2017). *n*: number of individuals; Mass (g): average adult body mass; Dive Depths include: Max. (m): absolute maximum dive depth; Ave. max (m): maximum dive depth averaged across all individuals; Ave. (m): mean dive depth; Dive Duration includes: Max (s); absolute maximum dive duration; Ave. max (s); maximum dive duration averaged across all individuals; Ave. (s): mean dive duration; Expected includes: Max depth (m): absolute maximum dive depth calculated by allometric equation (Burger 1991); Dive duration (s): expected average maximum dive duration calculated by allometric equation (Halsey et al. 2006b).

Species	Scientific name	*n*	Mass (g)	Dive Depth			Dive Duration			Expected		Reference
				Max (m)	Ave max (m)	Ave (m)	Max (s)	Ave max (s)	Ave (s)	Max depth (m)	Dive duration (s)	
Flesh-footed shearwater	*Puffinus carneipes*	3	609	66.5	–	4.8	–	–	–	64.9	–	Rayner *et al.* (2011)
Great shearwater	*Puffinus gravis*	2	863	18.9	–	2.9	40	–	6.95	72.5	33.8	Ronconi *et al.* (2010)
Sooty shearwater	*Puffinus griseus*	10	848	55.1	39.2	6.9	–	–	39.0	72.1	33.6	Dunphy *et al.* (2015)
Sooty shearwater	*Puffinus griseus*	9	850	69.9	–	15.9	100	–	–	72.1	33.7	Shaffer *et al.* (2009)
Balearic shearwater	*Puffinus mauretanicus*	19	508	28	–	4	69	–	10	61.3	28.5	Meier *et al.* (2015)
Hutton's shearwater	***Puffinus huttoni***	**6**	**350**	**35**	**14.7**	**5.3**	**67.5**	**35.7**	**19.2**	**54.5**	**25.2**	**This study**
Manx shearwater	*Puffinus puffinus*	36	421	55	33.1	9.6	–	46.2	13.5	57.8	26.8	Shoji *et al.* (2016)
Yelkouan shearwater	*Puffinus yelkouan*	7	500	30.2	19.1	–	–	–	–	61.0	–	Peron *et al.* (2013)
Cory's shearwater	*Calonectris borealis*	22	770	–	7.4	2	–	24.5	4	–	33	Paiva *et al.* (2010a)
Scopoli's shearwater	*Calonectris diomedea*	20	–	10	–	1.9	–	–	8.1	–	–	Grémillet *et al.* (2014)
Streaked shearwater	*Calonectris leucomelas*	13	513	6	–	–	18	–	–	61.5	28.6	Matsumoto *et al.* (2012)

Discussion

My results provide some of the first detailed information on the foraging behaviour of Hutton's shearwater while at sea. Hutton's shearwaters were found to forage almost exclusively during daylight hours, with only a few dives recorded at night, strongly suggesting these birds are visual predators (Paiva et al. 2010b; Raymond et al. 2010; Meier et al. 2015; Shoji et al. 2016). Although dives up to depths of 35 m were observed, approximately 70% of all dives were nearer the ocean's surface (≤ 5.6 m). The duration of dives averaged 19.2 s, but some dives reach a maximum duration of 67.5 s. The number of dives averaged 68.8 dives per day, with some birds undertaking as many as 2641 dives per foraging trip. Compared to dive depths and duration in other Procellariiforms, Hutton's shearwaters undertook shallower dives and of longer duration than expected by the allometric equation.

Diving depths

The average maximum dive depths I observed (15.0 m) in Hutton's shearwaters were within the range reported by Taylor (2008; 23.0 m ± 8.5 m; range 11.1–36.6 m), although his estimate was obtained with the capillary tube technique (Taylor 2008). I also found significant differences in diving depths with stage of breeding and time of day. There was a general decrease in the dive depths as breeding progressed with birds diving deeper in the incubation period, but then decreasing during the chick-rearing period. Greater average diving depths of incubating birds could be associated with individuals feeding on different prey or travelling to different foraging areas. In some seabirds, individuals travel further from their breeding colony at some stages of their breeding cycle to access more prey-enriched waters, rather than remaining close

to the colony, where prey are less abundant or of lower quality (Weimerskirch & Cherel 1998; Shaffer et al. 2009; Alonso et al. 2012; Cleeland et al. 2014). It may be that Hutton's shearwaters in the early incubation period alter their dive depths to select different prey species to replenish their body mass after egg laying or weight loss while incubating (Murphy 1996; Taylor 2008). Differences in diving depths at different times of the day could also be the result of foraging for different types of prey or in different areas. Unfortunately, I do not know exactly where Hutton's shearwater forage at different stages of their breeding cycle and at different times of the day, although some birds have been observed foraging 200 km east of the Canterbury coastline within the subtropical convergence zone (see Chapter 4) (Wragg 1985; Pinkerton 2011).

A significant difference was observed between the diving depths of Hutton's shearwaters between the early and late incubation and chick-rearing periods when I accounted for 'Date'. Thus, variation in dive depth was not due entirely to seasonal changes in the oceanic environment but with the differing demands of the breeding cycle. I could not determine the prey taken in the different stages of the breeding cycle or if this varied with dive depth, but this species is believed to feed on small fish, crustaceans and squid (Tarburton 1981; West & Imber 1985). An isotopic analysis of the Kaikōura near-shore food web compared to that of regrown tail feathers was also unable to establish the dietary preference of the Hutton's shearwater (see Chapter 3). In addition to differences in prey with dive depths, variability in diving depth may be affected by body mass recovery and energy requirements during incubation, chick-rearing and catering for post-hatch chick demands (Baduini & Hyrenbach 2003). Thus, the variability I observed in dive depths could be the result of

either changes in the need for individual maintenance of body condition or the provisioning demands of the chick.

As many species of potential prey migrate closer to the surface during the early morning and late evening, one might expect to see an increase in the depth of dives during the day as prey return to deeper water to avoid predation (Hays 2003). I observed the reverse pattern in most stages of the breeding cycle, especially during the late incubation and late chick-rearing periods. A possible explanation may be that the birds are changing the targeted prey species throughout the day (04:00–21:00 h), selecting a different prey size, foraging in a different location or alternatively, not all prey return to the ocean's depths and are still available in shallower waters (Sainmont et al. 2013). On the other hand, these shallower dives during the day may be consistent with shallow pursuit dives for pelagic prey. It should be noted that the TDRs I used are prone to error in shallow dives (<1.5 m), and this may have compromised my ability to detect very shallow foraging dives, and potentially biasing some of the diel pattern to deeper dives (Elliott et al. 2008; Raymond et al. 2010; Shoji et al. 2015; Shoji et al. 2016).

Foraging depths may also change over the breeding season as new resources become available. Greater diving depths have been recorded during the chick-rearing stage, compared to the incubation period, for the white-chinned petrel (*Procellaria aequinoctialis*) and black-vented shearwater (*Puffinus opisthomelas*), and this difference has been attributed to greater demands during this breeding stage (Keitt et al. 2000; Rollinson et al. 2014). Interestingly, the opposite was observed in the Hutton's shearwater with significantly shallower dives during the chick-rearing

period. It may be that incubating birds require different prey items to restore body fat reserves than those needed for feeding chicks (Elliott et al. 2008; Taylor 2008). During the chick-rearing period, prey items for self-maintenance may be either unsuitable for chicks, become unavailable, or are too energy intensive to collect. At present, I do not know if dive depths vary with distance from the colony (Weimerskirch & Cherel 1998; Elliott et al. 2008). Environmental conditions (seawater temperature, up-welling and currents) may also alter the abundance and prey type available (Chiswell & Schiel 2001; Meier et al. 2015) and thus dive depths.

Dive frequency

As with dive depth, dive frequency also varied with stage of breeding and time of day, but there was no effect of date, confirming this pattern was not due to just seasonal changes in the oceanic environment. An increase in dive frequency was observed around dawn and dusk during the early morning incubation and late evening chick-rearing periods, respectively (Figure 2.2). In contrast to the unexpected increase in depths of dives at these times, the concomitant increase in dive frequency is consistent with foraging activity changes in response to diurnal vertical migration of prey species responding to ambient light levels (Shaffer et al. 2009). Similarly, the increased diving frequency around 20:00 h during the chick-rearing period could be in response to mesopelagic prey returning to the surface waters during the evening. These surfacing prey species may be different, allowing adults to maximise hunting effort or to collect greater food quantities to provision their chick (Hays 2003; Raymond et al. 2010; Dias et al. 2016).

There was a significant decrease in foraging frequency between 18:00–20:00 h during the chick-rearing period; this behaviour may indicate various strategies. First, adults may use this time to find a suitable foraging location or to return to an area that has previously proven to be profitable in resource suitable for chicks provisioning (Cherel et al. 2002; Weimerskirch 2007). Although I have not investigated trip duration, studies have shown that adults collect prey for their chicks during both short and long expeditions but more energy is required to carry resources from a greater distances and relocating closer to the colony before foraging may be more advantageous (Weimerskirch 2007; Paiva et al. 2010b; Paiva et al. 2010a). Dietary differences between adults and chicks has been observed in several species, including the Cory's shearwater and blue petrel (*Halobaena caerulea*), which suggest different foraging strategies are used depending on whether the prey is for self-maintenance or feeding chicks (Cherel et al. 2002; Alonso et al. 2012). Second, this period of waiting may allow potential prey items to return to the surface waters, allowing for a reduction in energy expenditure and foraging effort. Finally, the reduced foraging frequency during the three-hour interval would allow time for adults to assimilate the previous meal and facilitate stomach clearing, allowing for maximum prey storage before hunting for chick provisioning (Alonso et al. 2012; Shoji et al. 2015).

Dive duration

Dive duration varied diurnally and between the incubating and chick-rearing periods (Fig. 2.4). The greatest dive durations were seen during the early incubation period where longer dives were observed early morning (05:00–07:00 h) and peaked again between 11:00 to 16:00 h. This pattern is opposite to that found in the White-chinned petrel where longer dives were undertaken during the chick provisioning period

(Rollinson et al. 2014). An increase in dive duration may be in response to pursuing larger or more nutritious prey to replace lost body mass through egg production or a long incubation bout (Baduini & Hyrenbach 2003). In addition, food items may be scarce, of a large size requiring additional handling, difficult to capture or at a greater depth than found during other times during the breeding season (Bianchi & Mislan 2016).

During the late incubation period, the foraging duration of each dive remained high during the early morning dives (05:00–10:00 h) but decreased significantly during the afternoon. Some predators select prey at more than one trophic level, and changes in foraging activity may indicate the availability of different species, energy-rich or more abundant prey items that are accessible earlier in the day (Sainmont et al. 2013).

Variability was also observed within the chick-rearing period where diving duration increased, especially between 06:00–07:00 and 11:00–16:00 h. This may indicate initial foraging early in the morning before relocating to another site at a greater distance from the colony. As I was not able to investigate where the individuals I used in this study foraged (since they were only fitted with TDRs), I was unable to consider how bathymetry, upwelling, currents or chlorophyll *a* conditions affect foraging behaviour, as is known in other seabirds (Baduini & Hyrenbach 2003). Dive duration did not change significantly during the late evening for any of the breeding periods, indicating prey items were either vertically migrating towards the surface and were more easily accessed by adults for self-provisioning or that sufficient prey items were obtained during shorter dives to provision their chick.

Diving behaviour compared to other Procellariiformes

The Hutton's shearwater is the lightest species within the group of Procellariformes for which detailed dive behaviour is available; these results show that they achieved deeper maximum and average daily diving depths and duration than some of the heavier species (Table 2.2). It has been proposed that diving depth and diving duration are strongly related to body mass (Halsey et al. 2006a; Halsey et al. 2006b; Dunphy et al. 2015), but this pattern is not totally weight-dependent as both the Balearic (*Puffinus mauretanicus*), Yelkouan (*Puffinus yelkouan*) and great (*Puffinus gravis*) shearwaters are heavier than the Hutton's shearwater yet they do not achieve, on average, greater depth or dive durations (Table 2.2) (Ronconi et al. 2010; Péron et al. 2013; Meier et al. 2015). If mass were the only contributing factor affecting dive depth and duration, then these shearwater species would be expected to attain similar depths and dive times as the sooty shearwater (Table 2.2).

By using the allometric equation for maximum dive depth from Burger (1991), Hutton's shearwater are predicted to dive to 54.5 m, compared to a maximum observed depth of 35.0 m. Similarly, the Balearic shearwater obtained shallower depths than calculated (Table 2.2) (Meier et al. 2015). This suggests that these birds did not need to forage at their maximal dive depth. In fact, it may be more energy efficient to hunt within shallower waters than to pursue prey at a greater depth when considering oxygen storage, anaerobic metabolism and the maintenance of the lactate threshold (Butler & Jones 1997; Ropert-Coudert & Wilson 2005; Butler 2006). Alternatively, birds may not dive as deep or as long as their physiology will allow if there is little competition for food, or energy expenditure is too high, it would be better to have a lower prey capture rate during a shallow dive than to endure the

metabolic cost of a higher catch rate at a greater depth (Halsey et al. 2006a). Conversely, the Manx (*Puffinus puffinus*) and sooty shearwaters obtained comparable depths as expected by allometry (Table 2.2) (Shaffer et al. 2009; Shoji et al. 2016).

Predicted dive duration in relation to body mass, potential oxygen storage and oxygen consumption illustrate a different story in Hutton's shearwater (Wilson et al. 1992; Halsey et al. 2006b; Dunphy et al. 2015). The expected average maximum dive duration for the Hutton's shearwater was 25.2 s, which is considerably less than the observed time of 35.7 s, indicating that this species can exceed the predicted dive limits, and may be part of a suite of adaptive behaviours for a highly pelagic lifestyle (Warham 1990). Likewise, the expected average maximum dive duration of the Manx and sooty shearwaters were also considerably less than the observed depth-duration (Table 2.2) (Shaffer et al. 2009; Shoji et al. 2016). Deep diving birds such as the sooty shearwater have lower respiratory oxygen stores than common diving (*Pelecanoides urinatrix*) and grey-faced petrels; this storage reduction is believed to help in decreasing buoyancy-related costs during deeper dives (Dunphy et al. 2015). In addition, the red blood cell count of sooty shearwaters was significantly higher than the two petrel species. Whether Hutton's shearwaters possess similar specialised physiological adaptations to allow longer dives is unknown, but would be worth investigating.

Conclusion

This study presents new data on the diving depth, duration and foraging frequency of the Hutton's shearwater. I detected significant differences in diving depths, diving durations and diving frequency during the incubation and chick-rearing periods and

over different times of the day, but there is little evidence of variation with date of the breeding period. These observed changes in foraging behaviour indicate different energetic requirements for adult breeding birds, chick provisioning, and potential changes in prey distribution and abundance. This study has provided information on the Hutton's shearwater diving behaviour and their ability to adjust to different foraging depths, but little is known about other aspects of their foraging behaviour. Further research is required to track Hutton's shearwater behaviour at sea, map their foraging locations and quantify dietary preference during the breeding and non-breeding periods. By understanding the Hutton's shearwater at sea behaviour, we can further understand potential environmental pressures and how to aid the conservation of this endangered species.

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Hutton's shearwater experimentally-induced tail feather regrown over the breeding season, 19 January 2015 (photo by Della Bennet).

Chapter 3

Sexual and seasonal dietary variation in the Hutton's shearwater (*Puffinus huttoni*) as revealed by stable isotope analysis

Abstract

Studies of the foraging behaviour of pelagic seabirds are difficult, but stable isotope analysis of feathers can provide an indirect method to investigate the general features of diet during the time the feathers were growing. I used the isotopic composition of normal and experimentally-induced feathers to compare the breeding and non-breeding diet of the Hutton's shearwater, an endangered seabird endemic to the Kaikōura region of New Zealand. The isotopic composition of feathers was then compared with potential prey items collected from the near-shore marine environment near the breeding colony. By applying trophic fractionation factors (2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$), and comparing the isotopic composition of the induced tail feathers and sampled prey items, I found that feather isotopic compositions were not consistent with a diet based on feeding locally. Both the $\delta^{13}C$ and $\delta^{15}N$ from zooplankton and fish collected within 8 km of Kaikōura were significantly different than the isotopic composition of induced feathers and were outside of the range expected for consumed local prey items. To determine if Hutton's shearwaters were feeding outside of the near-shore ecosystem, I compared induced feather isotopic compositions to potential prey items in the adjacent Banks Peninsula area (~100 km south). The isotopic composition of these potential prey items were consistent with induced feathers, suggesting Hutton's shearwaters may be foraging

offshore of Banks Peninsula during the breeding period. A significant segregation in the $\delta^{13}C$ and $\delta^{15}N$ tail feather values determined between the breeding (i.e., induced feathers) and non-breeding periods confirmed that feathers grown during the non-breeding period are not the result of local feeding but likely from sources in the Indian Ocean, off Western Australia. Sexual differences in isotopic composition were also detected during the non-breeding period, suggesting spatial or temporal resource partitioning between the sexes while on the non-breeding grounds. Stable isotope analysis can provide insight into the foraging behaviour, and sexual segregation, demonstrating the importance of isotopic research to the conservation and protection of endangered seabirds with large geographic ranges.

Introduction

Dietary studies can be difficult in highly pelagic seabirds which spend long periods of time at sea. Direct collection techniques can be invasive (Barrett et al. 2007), and these samples may not be representative, or may be limited in temporal and spatial scope. Even when samples are obtained, prey remains can be difficult to identify, as many prey items may be partially digested (West & Imber 1985). This leads to a potential bias towards organisms that have been consumed more recently or less easily digested species (Barrett et al. 2007).

Stable isotope analysis (SIA) is a powerful ecological tool that can be used to indirectly investigate the diet of seabirds during the breeding and non-breeding period (Inger & Bearhop 2008). For example, feathers collected as birds return to the breeding grounds reflect the diet during the non-breeding period (where the feathers were grown), while forced regrown feathers that were induced on the breeding

grounds can provide an estimate of the breeding diet through local nutrient assimilation (Quillfeldt et al. 2005). By applying different fractionation effects associated with the metabolism of prey items of known isotopic composition, it is possible to investigate sexual, spatial, and temporal variation in diet and infer the trophic position of a species (Rau et al. 1992; Quillfeldt et al. 2005; Gladbach et al. 2007; Caut et al. 2009; Phillips et al. 2009).

Pelagic seabirds in the Order Procellariiformes (albatrosses, shearwaters and petrels) occur in most of the world's oceans, and many temperate-breeding species make trans-equatorial migrations between the breeding and non-breeding period (Warham 1990). Unlike these species, the Hutton's shearwater (*Puffinus huttoni*) remains predominantly within the Southern Hemisphere and migrates from its breeding grounds in Kaikōura, South Island, New Zealand to the Indian Ocean, Western Australia during the non-breeding period (Halse 1981). Although details of its movements are poorly known, adult Hutton's shearwaters undergo their post-nuptial moult during the non-breeding period, presumably while in the Indian Ocean (Robinson 1973; Halse 1981; Marchant & Higgins 1990).

The Hutton's shearwater is classified as "endangered" (IUCN Red List) and has recently been relisted from "at-risk and declining" to "threatened and nationally vulnerable" under the New Zealand Threat Classification (Birdlife International 2017; Robertson et al. 2017). This species has undergone recent range restriction and decline in population size due to mammalian predation, predominantly feral pigs (Cuthbert 2002). The Hutton's shearwater predominantly spend their life at sea, only returning to their natal grounds to breed (Halse 1981). It nests solely in the Seaward

Kaikōura Ranges (Harrow 1965), although a new population has been established at a lowland site on the Kaikōura Peninsula (Rowe 2014). Most research on the Hutton's shearwater has focused on monitoring population size, assessing levels of predation, and improving conservation efforts within the alpine colonies (Cuthbert 2001), but little is known about the foraging behaviour and diet of this species, either on their breeding or non-breeding grounds.

In this study, I investigated the diet of Hutton's shearwaters by using isotopic fractionation between their tail feathers and potential prey. My objective was to identify potential foraging locations of birds while at sea, and any seasonal and sexual differences in diet. I used $\delta^{13}C$ and $\delta^{15}N$ values of induced tail feathers to compare potential dietary isotopic composition from two potential foraging areas (Kaikōura and Banks Peninsula), and with feathers grown on the non-breeding grounds. I also assessed variation between the two breeding colonies (alpine versus coastal) and between sexes on the non-breeding grounds.

Methods

Ethical statement

This study was performed with permission of the Department of Conservation (DOC). Permits were provided by the DOC (WAA-38708-FAU) and the University of Canterbury Animal Ethics Committee (2014/20R).

Feather collection and prey sampling

During the 2014–15 breeding season, adult Hutton's shearwater tail feathers were collected from the alpine Kowhai River colony (>1200 m.a.s.l; *n* = 34 feathers) and the coastal Kaikōura Peninsula (Te Rae O Atiu, ~80 m.a.s.l; *n* = 28 feathers) colony for stable isotope analysis. From mid November-early December 2014, birds were captured, and a single tail feather (rectrices R5) was removed from each adult. These first-plucked feathers were grown on their non-breeding grounds, presumably in the Indian Ocean (Halse 1981; Marchant & Higgins 1990). In January 2015, I then collected the induced regrown feathers. Leg band number was used to identify birds and the same tail feathers (R5) were collected. As induced feathers were grown while birds were on the breeding grounds, their isotopic signature should reflect the local diet. All feathers were stored in individual paper envelopes for approximately six months before being prepared for analyses. Each feather was cleaned of surface contaminants using 2:1 chloroform:methanol, rinsed in nano-pure deionised water and air-dried in glass vials with silicon natural/PTFE septa EPA caps.

To determine the $\delta^{13}C$ and $\delta^{15}N$ values of potential shearwater prey items (zooplankton and fish), samples were collected in an oblique tow using a box-pyramid design plankton net (250 μm). Tows were run between November 2014 and January 2015. The tow was run behind the boat from a depth of 50 m and the net was gradually winched to the surface over a 10 min period. The samples were collected between two to eight km off the Kaikōura coast and close to the date of the next new moon. Samples collected coincided with the period in which the birds were regrowing the induced feathers. Tow samples were sorted into one of nine groups (amphipod, cephalopod, crustacean larvae, copepod, euphausiid, munidae, mysis, stomatopod,

and fish), and dried at 55ºC. Zooplankton samples collected from the off-shore Banks Peninsula area were sampled using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Decima, *unpubl. data*). From a single tow (R/V Tangaroa, National Institute of Water and Atmospheric Research [NIWA]), mixed zooplankton species were collected between 5–50 m (6–12/12/05) and were isotopically analysed. The samples from off-shore Banks Peninsula were collected by NIWA and used here for comparative purposes (Moira Decima, pers. comm.)

Isotopic analyses

To run the isotopic analyses, individual samples of fish, zooplankton and feather vane sections were finely chopped, weighed to 500 micrograms (± 100 µg) and placed into tin capsules (OEA Laboratories 8mm x 5mm). Samples were analysed for $\delta^{13}C$, $\delta^{15}N$, %C and %N using a continuous-flow isotopic-ratio mass spectrometry. Data were normalised to Vienna PeeDee Belemnite for $\delta^{13}C$ and Air for $\delta^{15}N$ based on replicate analyses of certified reference materials IAEA-N-1, IAEA-N-2, IAEA-CH-3, NBS22, NBS19 in each analytical sequence. Results are expressed in conventional δ-notation (Hobson 2005).

Statistical analyses

Tail feather isotope values were estimated in a linear mixed-effects model framework (R package lme4, version 1.1-7, Bates et al. 2015), using R version 3.3.0. Separate models were assumed for carbon and nitrogen isotope compositions. Model selection was performed using the Akaike's Information Criterion (AIC_c) to determine the best model (R package boot, version 1.3-18). Differences in $\delta^{13}C$ between sex were examined by analysis of variance (ANOVA). Unless otherwise stated, all values are

presented as predicted 95% confidence intervals. I have applied caution when assessing the feather isotopic composition compared to the potential food items $\delta^{13}C/\delta^{15}N$ values by using various trophic fractionation factors (e.g., 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$) (Cherel et al. 2005b; Caut et al. 2009).

Results

Isotopic composition of feathers

The average values of $\delta^{13}C$ and $\delta^{15}N$ for Hutton's shearwater tail feathers are shown in Figure 3.1 and summarised in Table 3.1. Both natural and induced tail feather samples were enriched in $\delta^{13}C$ and $\delta^{15}N$ compared to potential prey values with the magnitude of enrichment depending on the fractionation factor used (2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$). Variability was observed also between months for $\delta^{13}C$ and $\delta^{15}N$ prey and feather values. The average $\delta^{13}C$ larval fish and zooplankton values were less enriched compared to the induced tail feathers collected during the breeding season (Table 3.1).

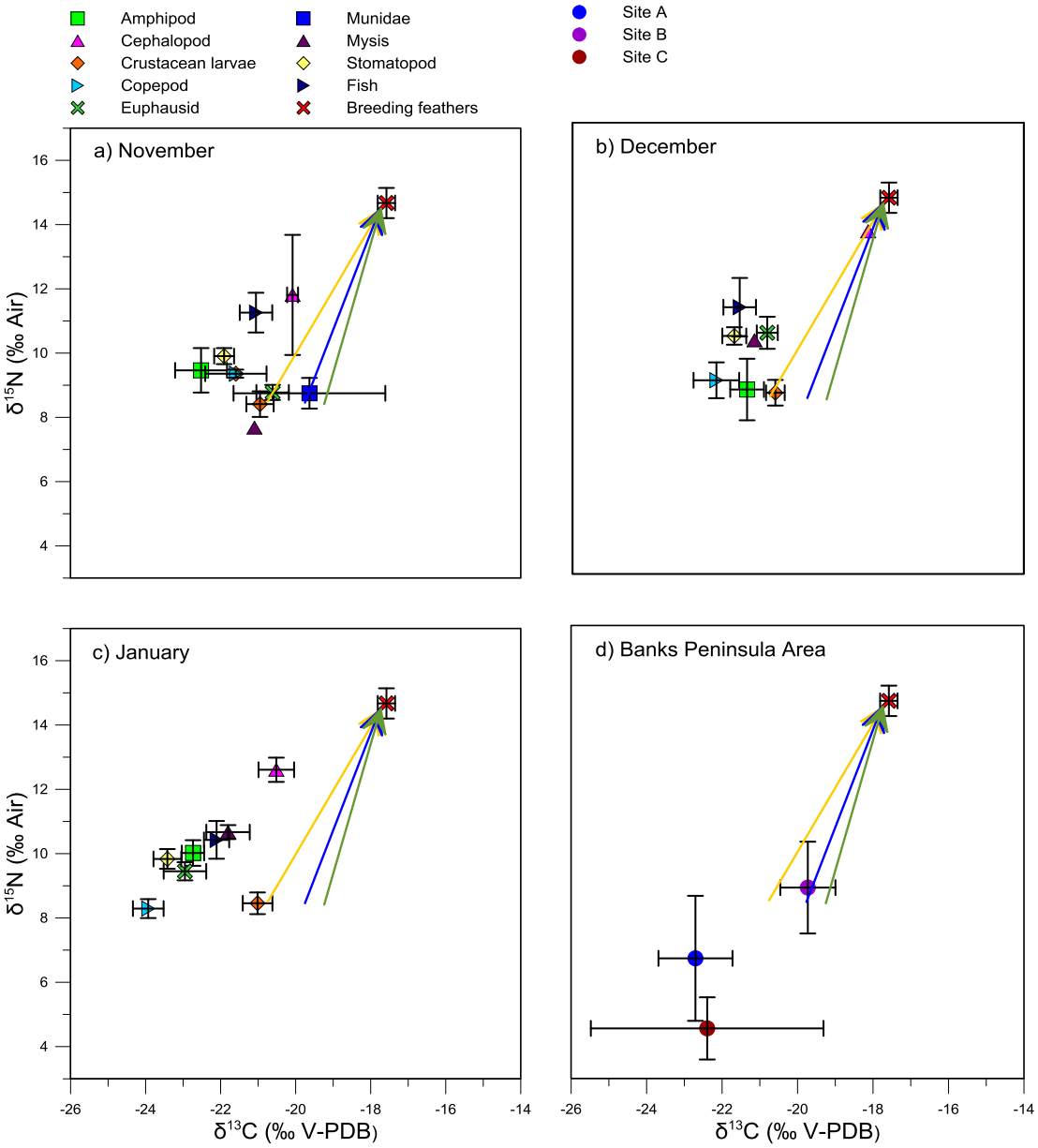

Figure 3.1 Stable isotope compositions for zooplankton and fish and the isotopic composition of Hutton's shearwater tail feathers (mean ± CI and individual values). Feather data plotted include samples from both the Kaikōura alpine and peninsula sites. Plankton tow samples collected monthly (2014–15) from the near-shore Kaikōura coastline a) November, b) December (crustacean larvae obscured by arrows), and c) January compared to regrown breeding season tail feather $\delta^{13}C$ / $\delta^{15}N$ values; d) Zooplankton (December 2015; Decima, *unpubl. data*) collected from offshore waters (site A -44.1473S, 174.039E; site B -43.519S, 174.573E; site C -43.236S, 175.865E), east of the Banks Peninsula compared to regrown breeding season tail feather $\delta^{13}C$ / $\delta^{15}N$ values. The arrows indicate the 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ (yellow 2‰, blue 3‰ and green 4‰ increase in $\delta^{15}N$).

Table 3.1 Summary of $\delta^{13}C$ and $\delta^{15}N$ values (mean ± CI) for fish, zooplankton and Hutton's shearwater adult tail feathers sampled during 2014–15. BP = zooplankton collected from offshore waters, east coast of the Banks Peninsula area; all other samples are from the Kaikōura near-shore waters; non-breeding feathers were moulted and replaced during the winter period; and breeding season feathers were induced and regrown during this study.

Sample	Season	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
		Mean ± CI	Range (‰)	Mean ± CI	Range (‰)
Fish	November (*n* = 18)	–21.06 ± 0.40	–18.67 to –24.24	11.26 ± 0.57	12.54 to 7.42
	December (*n* = 12)	–21.55 ± 0.39	–17.29 to –23.51	11.27 ± 0.81	14.67 to 6.02
	January (*n* = 31)	–22.11 ± 0.32	–19.09 to –24.88	10.43 ± 0.56	13.37 to 7.10
Zooplankton	November (*n* = 66)	–21.34 ± 0.29	–19.56 to –22.21	9.26 ± 0.24	13.33 to 9.12
	December (*n* = 57)	–21.19 ± 0.25	–20.66 to –22.71	9.67 ± 0.35	12.32 to 7.18
	January (*n* = 82)	–22.32 ± 0.29	–20.49 to –23.64	9.74 ± 0.30	14.01 to 8.43
	December: BP (*n* = 20)	–21.14 ± 0.88	–17.44 to –24.00	7.26 ± 1.01	10.83 to 3.73
Feathers	Non-breeding (*n* = 31)	–17.58 ± 0.22	–16.06 to –18.71	14.67 ± 0.45	16.43 to 11.13
	Breeding (*n* = 31)	–17.15 ± 0.18	–16.06 to –18.23	13.02 ± 0.32	14.36 to 10.47

The isotopic composition of the non-breeding feathers and the induced feathers regrown during the breeding season are summarised in Table 3.2. The most parsimonious models selected to describe the $\delta^{13}C$ and $\delta^{15}N$ values included 'Sex and Season' and 'Season,' respectively, as a fixed effect. 'Nest' and 'Band' were used as random effect (Table 3.3). A significant difference was detected in the mean $\delta^{13}C$ and $\delta^{15}N$ tail feather values between the breeding (intercept; Std. Est. –17.30, [CI –17.58, –17.06]; intercept; Std. Est. 14.67, [CI 14.29, 15.02] respectively) and non-breeding seasons (Std. Est. 0.44, [CI 0.22, 0.66]; Std. Est. –1.65, [CI –2.09, –1.13] respectively; Figure 3.2). I found no effect of colony location (alpine and peninsula) on $\delta^{13}C$ or $\delta^{15}N$ values of feathers during the breeding or non-breeding periods (Table 3.3). There was also no significant variation observed in the interaction between sex and location (Table 3.3).

Table 3.2 Summary of feather $\delta^{13}C$ and $\delta^{15}N$ values (mean ± CI) for Hutton's shearwater adults sampled during 2014–15. Non-breeding feathers were moulted and replaced during the winter period. Breeding season feathers were regrown due to study sampling protocols (see text).

Sex	Location	Season	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
			Mean ± CI	Range (‰)	Mean ± CI	Range (‰)
Male	Peninsula (*n* = 7)	Non-breeding	–17.27 ± 0.47	–16.82 to -18.23	13.10 ± 0.18	12.01 to 13.83
		Breeding	–17.82 ± 0.53	–16.86 to -18.48	14.93 ± 0.20	13.7 to 15.99
	Alpine (*n* = 13)	Non-breeding	–17.35 ± 0.21	–16.73 to -17.84	12.98 ± 0.06	10.49 to 14.36
		Breeding	–17.64 ± 0.38	–16.64 to -18.71	14.37 ± 0.11	11.13 to 16.00
	Combined (*n* = 20)	Non-breeding	–17.32 ± 0.19	–16.73 to -18.23	13.02 ± 0.04	10.49 to 14.36
		Breeding	–17.70 ± 0.28	–16.64 to -18.71	14.56 ± 0.06	11.13 to 16.00
Female	Peninsula (*n* = 7)	Non-breeding	–16.95 ± 0.45	–16.38 to -17.96	12.79 ± 0.17	10.47 to 13.72
		Breeding	–17.30 ± 0.59	–16.08 to -18.08	14.88 ± 0.22	12.90 to 16.43
	Alpine (*n* = 4)	Non-breeding	–16.60 ± 0.94	–16.06 to -17.47	13.39 ± 0.47	13.10 to 13.92
		Breeding	–17.45 ± 0.91	–16.89 to -18.38	14.83 ± 0.46	13.44 to 15.92
	Combined (*n* = 11)	Non-breeding	–16.82 ± 0.38	–16.06 to -17.96	13.01 ± 0.11	10.47 to 13.92
		Breeding	–17.36 ± 0.42	–16.08 to -18.38	14.86 ± 0.13	12.90 to 16.43

Table 3.3 Comparison of linear mixed-effects models to explain carbon and nitrogen tail feather isotopic composition values. Selected models are in bold. 'Band' and 'Nest' were used as random variables for all models. Log likelihood = natural logarithm of the maximum likelihood for the model; AIC_c = Akaike Information Criterion model score; ΔAICc = difference in Akaike Information Criterion score between models; Weight = Akaike Information Criterion weights.

Model	d.f.	Log Likelihood	AICc	ΔAICc	Weight
Carbon					
(Area + Season + Sex)^2	10	–52.11	128.54	14.29	0.001
(Area + Sex) ^2	7	–56.13	128.33	14.07	0.001
(Area + Season) ^2	7	–54.76	125.60	11.34	0.002
(Season + Sex) ^2	7	–50.65	117.38	3.12	0.136
Area + Season + Sex	7	–51.13	118.34	4.08	0.084
Area + Sex	6	–55.96	125.45	11.20	0.002
Area + Season	6	–54.29	122.10	7.85	0.013
Season + Sex	**6**	**–50.36**	**114.25**	**0.00**	**0.647**
Area	5	–58.61	128.28	14.03	0.001
Season	5	–53.54	118.15	3.89	0.092
Sex	5	–55.21	121.50	7.24	0.017
Null	4	–57.86	124.42	10.16	0.004
Nitrogen					
(Area + Season + Sex) ^2	10	–92.28	208.87	9.38	0.005
(Area + Sex) ^2	7	–107.31	230.69	31.20	0.000
(Area + Season) ^2	7	–93.48	203.04	3.56	0.090
(Season + Sex) ^2	7	–93.85	203.78	4.30	0.062
Area + Season + Sex	7	–94.44	204.95	5.47	0.035
Area + Sex	6	–108.28	230.09	30.60	0.000
Area + Season	6	–94.34	202.21	2.72	0.136
Season + Sex	6	–94.31	202.15	2.67	0.140
Area	5	–108.29	227.65	28.16	0.000
Season	**5**	**–94.21**	**199.49**	**0.00**	**0.532**
Sex	5	–108.26	227.59	28.10	0.000
Null	4	–108.25	225.21	25.72	0.000

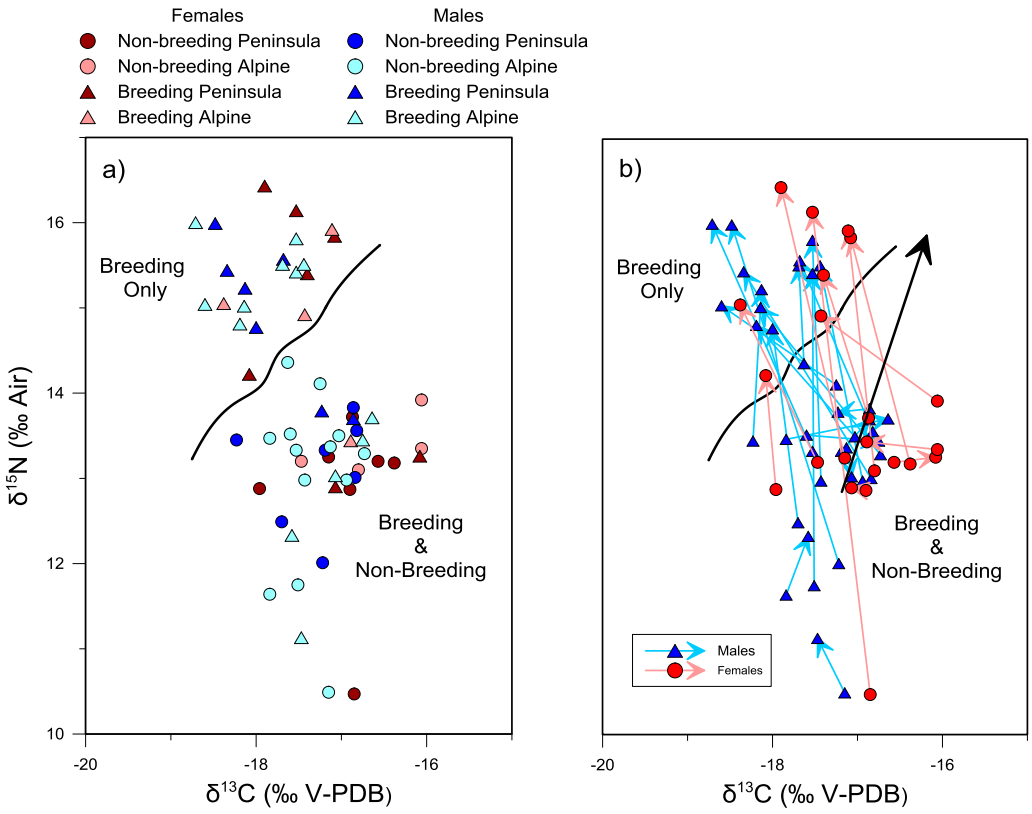

Figure 3.2 Stable isotope compositions ($\delta^{13}C$ / $\delta^{15}N$ values) for Hutton's shearwater tail feathers grown during the breeding (induced) and non-breeding seasons. Feather data plotted include samples from both the Kaikōura alpine and peninsula sites. a) Variation in isotopic ratios of carbon and nitrogen between the different breeding periods independent of sex or colony. b) Isotopic change in carbon and nitrogen values from the non-breeding to the breeding period. The direction and magnitude of change in diet are not consistent with moving up an isotopically similar food chain and illustrates two distinct foraging areas. The black arrow indicates a 3‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$.

A significant difference was detected in the mean $\delta^{13}C$ values between feathers collected from females (intercept; Std. Est. –17.30, [CI –17.58, –17.06]) and males, and this was independent of season (Std. Est. –0.43, [CI –0.72, –0.15]). An ANOVA detected a significant difference in the $\delta^{13}C$ values between male (M) and female (F) tail feathers during the non-breeding period ($F_{1,29} = 8.01$, $P < 0.01$), but no significant difference in the induced tails feathers during the breeding season ($F_{1,29} = 2.19$, $P = 0.15$). The range in $\delta^{13}C$ isotopic composition was greater during the breeding season (F = 2.30‰, M = 2.07‰) than the non-breeding season (F = 1.87‰, M = 1.15‰).

Less variability was observed in the $\delta^{15}N$ composition during the breeding (F = 3.53‰, M = 4.87‰) and non-breeding periods (F = 3.45‰, M = 3.87‰), but I found no evidence of variation in the $\delta^{15}N$ values between sexes.

Isotopic composition of potential prey

The composition of potential food items varied over the season and between collecting areas near Kaikōura and Banks Peninsula (Figure 3.1, Table 3.1). Values of $\delta^{13}C$ and $\delta^{15}N$ from samples collected between November to January overlapped extensively, but I observed a negative shift in the average $\delta^{13}C$ values of zooplankton from –21.34‰ in November to –22.32‰ in January, and of fish from –21.06‰ to –22.11‰, in the same time period (Table 3.1). The $\delta^{15}N$ values for fish was initially 11.26‰ in November and 11.27‰ in December, before declining to 10.43‰ in January, whereas $\delta^{15}N$ values for zooplankton increased and remained high over the same period (9.26 to 9.74‰, respectively). The zooplankton samples collected off the east coast of Banks Peninsula during December (–21.14‰) were comparable to the Kaikōura $\delta^{13}C$ value but were of a lower $\delta^{15}N$ value (6.69‰).

Discussion

Here, I show the first known foraging segregation between male and female Hutton's shearwaters. My results demonstrate dietary variation between seasons and between the sexes in the non-breeding period, but no variation was detected between the two breeding colonies. The apparent lack of local foraging within the Kaikōura near-shore area was not expected. Despite the range in available prey and the overlap in species between months, the isotopic signatures from the induced Hutton's shearwater

feathers were not consistent with foraging on the local food web and an increase between the fractionation factors did not explain the observed feather enrichment. Instead, my results indicate the Hutton's shearwater likely forage at some distance from the Kaikōura region and the isotopic signatures are more comparable to isotopic ratios from prey collected ~100 km south towards Banks Peninsula.

As anticipated, a significant difference was detected between the $\delta^{13}C$ and $\delta^{15}N$ isotopic composition for the breeding and non-breeding tail feathers. This confirms that the Hutton's shearwater leave the Kaikōura region and most likely to spend winter in the Indian Ocean (Halse 1981; Warham 1990). However, the difference between the sexes during the non-breeding period was not expected. Previous studies of other shearwaters have typically recorded sexual segregation during the breeding season and in dimorphic species, not in relatively monomorphic species like the Hutton's shearwater.

The reliability of isotopic analyses to describe the diet and trophic level of seabirds depends on several assumptions, and ambiguities associated with trophic fractionation factors is an important unresolved problem in stable isotope ecology (McCutchan et al. 2003; Boecklen et al. 2011). Predator tissues are typically thought to be 2–4‰ enriched in ^{15}N, and 1‰ enriched in ^{13}C, when compared to known prey item compositions (Hobson et al. 1994; Cherel et al. 2005b). However, great care must be taken when applying a fractionation model to a species, especially when no control feeding experiment has been carried out (Cherel et al. 2005b). Previous studies have shown variability from marginal trophic enrichment in $\delta^{13}C$ for wild birds (Rau et al. 1983; Hobson & Welch 1992; Hobson et al. 1994) through to 4–6‰ $\delta^{13}C$ in

controlled diets in captive-reared species (Mizutani et al. 1992; Cherel et al. 2005b; Bushman 2016). Captive species are fed a controlled diet that is readily obtainable but may not necessarily be consumed naturally in the wild (Hobson & Clark 1992a; Kelly 2000; Bushman 2016). For example, fractionation factors for king (*Aptenodytes patagonicus*) and rockhopper (*Eudyptes chrysocome*) penguin feathers ranged between 3.49–4.4‰ $\delta^{15}N$ and <1‰ in $\delta^{13}C$ for a controlled diet containing whole fish (Atlantic herring, *Clupea harengus* and Icelandic capelin, *Mallotus villosus*) (Cherel et al. 2005b). This shows the complexity and potential variation found between a consumer and the evaluated diet (Bearhop et al. 2002). As no controlled feeding experiment has been undertaken for the Hutton's shearwater, I assumed a 1‰ increase in $\delta^{13}C$ for every increase in trophic level.

Setting rates of isotopic enrichment between different trophic levels may vary, and setting a single fractionation value may influence the interpretation of the food web (Hobson & Welch 1992; Linnebjerg et al. 2016). For example, the fractionation factor for breast feathers sampled from four penguin species varied between 2.1–4.8‰ in $\delta^{15}N$ for wild and captive fed individuals (Mizutani et al. 1992; Cherel et al. 2005c; Cherel et al. 2005b; Polito et al. 2011). Hence, I used a range of $\delta^{15}N$ values (2–4‰) to account for the variation found within each trophic level, allowing for any potential error (Cherel et al. 2005b). By selecting discrimination factors between potential prey items and the consumers tissues (i.e., feathers), I was able to investigate the possibility that the predator species had consumed a diet or mixed diet from the sampled prey collected from the sampled location (Hobson 1993; Cherel et al. 2005b; Labbé et al. 2013).

The isotopic composition of potential prey species varied between months. When compared to the values of $\delta^{13}C$ and $\delta^{15}N$ in Hutton's shearwater tail feathers, the best fractionation model (2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$) observed between the induced tail feathers and the Kaikōura near-shore samples was a 2‰ increase in $\delta^{15}N$. I found the greatest number of prey species observed was during the November plankton tows for the 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ (Figure 3.1a). The 2‰ increase in $\delta^{15}N$ for November and December indicated cephalopod and crustacean larvae prey but changed to munidae and cephalopods, respectively (Figure 3.1a, b) for the 3–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$. Only crustacean larvae were identified as potential prey for the 2‰ increase in $\delta^{15}N$ for the plankton tows in January (Figure 3.1c). A potential trophic relationship was observed for the induced feather composition following the 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ between the zooplankton collected offshore (80–200 km) from Banks Peninsula (2015; Decima, *unpubl. data*), during the breeding period (Figure 3.1d). These results suggest that the Hutton's shearwater predominantly forage further south than previously expected, although the actual food resources have not been identified. The current available literature suggests Hutton's shearwater forage on small fish, crustacean and squid (Harrow 1976; Tarburton 1981; West & Imber 1985).

There are several ways the Hutton's shearwater tail feather stable isotopic compositions can be interpreted. First, through foraging behaviour; second, physiological and metabolic effects; and third, spatial and temporal effects.

Foraging behaviour

During the breeding season, foraging locations may vary depending on the chick's requirements and self-maintenance (Cherel et al. 2005a). My analysis of zooplankton and larval fish samples collected during the breeding season from the Kaikōura near-shore demonstrated that different potential prey items can be identified if nitrogen isotope trophic fractionation ranged between 2 and 4‰ for each 1‰ increase in $\delta^{13}C$. Several potential prey items were identified during the different months and these varied across the range in $\delta^{15}N$ values (Figure 3.1). For example, November prey samples included cephalopods and a variety of crustaceans for all fractionation factors, but no fish were detected. However, this pattern did not continue in December or January (Figure 3.1a-c). If shearwaters were utilising a 2‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$, the availability of prey species remains plausible but greatly reduces as the $\delta^{15}N$ values increases. It is difficult to clearly associate a fractionation model with the tail feather isotopic composition over the 3‰ and 4‰ $\delta^{15}N$ increase considering that no prey items were observed within the 10–13‰ isotopic ranges. This suggests that the shearwaters may be predominantly foraging outside of the near-shore coastal system near the breeding colonies at Kaikōura or, more unlikely, they were foraging in the Kaikōura area but not feeding on the prey items sampled during the collection period.

There are a variety of possible explanations for the discrepancy detected within these results. First, a lot of variability in stable isotope analysis remains unexplained (Boecklen et al. 2011) and caution is needed when selecting enrichment factors, especially for a wild species where no controlled experiment has been undertaken (Cherel et al. 2005b). Conducting experimental feeding trials on wild seabirds is not

feasible as these animals would need to be monitored for months, or years (Hobson & Clark 1992b; Cherel et al. 2005b). Second, the rate of fractionation and dietary change detected in tissues may also vary due to metabolic rate, stress, fasting, and physical activity of the species (Hobson & Clark 1992b; Cherel et al. 2005c; Cherel et al. 2005b). Wild animals actively forage to acquire resources whereas captive animals are provided food in a more passive manner (Hobson & Clark 1992a; Bond & Jones 2009). It has been suggested that marine animals increase in $\delta^{15}N$ by 3 to 4‰ per trophic step (Peterson & Fry 1987; Rau et al. 1992; Kelly 2000; Cherel et al. 2005b), but this does not match with my results. Third, depending on the selected prey type, the estimated fractionation and trophic shift in N can greatly vary (e.g., invertebrates +1.4‰, alga and plants +2.2‰, vertebrates +3.3‰; (McCutchan et al. 2003). In addition, depending on the proportion of each prey type consumed, the fractionation values may under- or over-estimate the consumer's trophic position, and this uncertainty increases for each additional rise in trophic step (McCutchan et al. 2003; Caut et al. 2009). Lastly, the type of tissue used (e.g., muscle or whole organism) and how the sample is analysed (acidified or unaltered samples) can also affect the C isotopic shift (McCutchan et al. 2003). For example, $\delta^{13}C$ values of muscle tissue can become more positive due to lipid extraction, whereas, whole organisms showed a significantly higher carbon value when untreated. Furthermore, a compound-specific isotopic amino acid study by Steffan et al. (2013) established a fractionation increase of +7.6‰ $\delta^{15}N$, and when compared to bulk nitrogen analysis, the predicted trophic level was underestimated on average by 1.11‰ $\delta^{15}N$. A future study addressing compound-specific isotopes may be beneficial in establishing the Hutton's shearwater trophic discrimination factor.

Understanding the spatial distribution of a species will enable a more accurate assessment of potential diet. Hutton's shearwaters have been observed flying off the coast of Banks Peninsula and foraging near the Chatham Rise during the breeding season (A. Crossland, and A. Spencer, *pers. comm*.; Pinkerton 2011). By comparing the isotopic composition of zooplankton species collected (Decima, *unpubl. data*) between 20–220 km off the coast of Banks Peninsula (Figure 3.1d), $\delta^{13}C$ and $\delta^{15}N$ zooplankton values are similar to the induced tail feathers and may represent prey items of the Hutton's shearwater diet. I cannot discount that Hutton's shearwater may forage at further distances while incubating their egg, but then forage closer to the nest site when provisioning their chick (Cherel et al. 2005a). Through this scenario, the induced tail feathers would indicate foraging outside of the Kaikōura region and would not represent prey items collected for the chicks as birds do not forage for themselves and rely on energy stores (Cherel et al. 2005a).

Physiological and metabolic effects

No significant difference was detected for $\delta^{13}C$ or $\delta^{15}N$ values during the breeding period, suggesting both sexes have a similar diet and comparable foraging success (Figure 3.2). This is consistent with the lack of sexual dimorphism detected in the Hutton's shearwater although a weak increase (5.4–7.7%) was observed in the weight of adult male birds when assessed by Storer's sexual dimorphism index (Storer 1966; Cuthbert & Davis 2002; Bull et al. 2005; Navarro et al. 2009). Dimorphic species may utilise morphological adaptations, such as differences in body weight, to access different food resources (Quillfeldt et al. 2011; Cleasby et al. 2015) or bill structure (González‐Solís et al. 2000; González‐Solís 2004). The advantages of sexually dimorphic adaptations are more evident during the breeding season for most species

(González‐Solís et al. 2000; Phillips et al. 2009; Quillfeldt et al. 2011; Cleasby et al. 2015), but this was not the case in the Hutton's shearwater (Figure 3.2a).

Although I have not tested nitrogen recycling or egg/yolk composition (Hobson 1995), the lack of sexual differences in isotope composition in the breeding season suggests that sex is not playing a part in determining diet preference or individual choice (Hedd et al. 2014). Nonetheless, a few birds did display a $\delta^{13}C$ composition that is comparable to that of the non-breeding environment (Figure 3.2a). This suggests a potential degree of flexibility and plasticity of these individuals in selecting foraging areas that are different from the other shearwaters (Dias et al. 2011). Similarly, when comparing the variation in $\delta^{13}C$ or $\delta^{15}N$ values from the non-breeding to the breeding period, the direction of increase and magnitude of change is inconsistent with some males and females foraging within an isotopically similar food web (Figure 3.2b). This significant difference implies the breeding, and non-breeding areas have different baseline or isotopic bulk carbon and nitrogen compositions, and that these compositions can be used to indicate spatial and temporal changes in locations (Vander Zanden & Rasmussen 2001; Post 2002; Gladbach et al. 2007; Ramos et al. 2015).

Spatial and temporal effects

I found a significant difference $\delta^{13}C$ and $\delta^{15}N$ values between the breeding and non-breeding periods (Figure 3.1d, 3.2), indicating a spatial and temporal segregation. Through observations of birds at sea, and surveys of beach-wrecked birds, it is thought that the Hutton's shearwater circumnavigates Australia during the non-breeding season, overwintering and foraging in the Indian Ocean (Halse 1981;

Warham 1981; Reed & McKean 1982; Asmussen 2006). This latitudinal movement provides a natural isotopic gradient in $\delta^{13}C$ values from which foraging locations and potential moult sites can be inferred (Quillfeldt et al. 2005; Gladbach et al. 2007). By using the $\delta^{13}C$ and $\delta^{15}N$ values of other procellariiform species, I was able to infer 'a potential' foraging area for Hutton's shearwaters during the non-breeding period that was clearly not in the Kaikōura area. Although I cannot directly confirm with my isotopic analyses that birds were spending the non-breeding period in the Indian Ocean (as I did not sample potential prey from this region), my results were nonetheless consistent with birds foraging at latitudes at which they have been observed in the Indian Ocean. However, the geographic range covered during this time is unknown, nor is it known how long birds spend in each area while on migration. The isotopic $\delta^{13}C$ values of the Hutton's shearwater I found are similar to the Antarctic prion (*Pachyptila desolata*), and wandering (*Diomedea exulans*), black-browed (*Thalassarche melanonphris*) and Indian yellow-nosed albatrosses (*T. carteri*), which are known to forage in the temperate waters north of the Subtropical Front (Cherel et al. 2006; Jaeger et al. 2013; Quillfeldt et al. 2015; Polito et al. 2017). This suggests that Hutton's shearwaters are similarly foraging during the non-breeding period in the same types of environment as these species.

I found a significant difference in $\delta^{13}C$ values between the sexes in the non-breeding season, suggesting spatial segregation of foraging habitat while the birds are in the Indian Ocean. Sexual segregation during the non-breeding period is thought to be less common as resource competition is not concentrated near the breeding areas as it is during the breeding season, allowing individuals to forage on the same resources (Phillips et al. 2009). The detected variability found in Hutton's shearwater feathers

might be a result of temporal separation whereby the females forage in more productive, warmer waters to acquire the necessary nutrients for egg formation, whereas males return sooner to the breeding colony (Hedd et al. 2014). Alternatively, competition avoidance through geographic separation has been observed between the sexes of large albatross and giant petrel species during the non-breeding period, but not amongst the smaller petrel species (Phillips et al. 2009). Depending on the mechanism that has lead to the $\delta^{13}C$ composition difference between the sexes, this may be the first evidence of geographic segregation in Hutton's shearwaters during the non-breeding period. To investigate further, compound-specific stable isotope analysis using amino acids may be beneficial in establishing the Hutton's shearwater geographic separation (Steffan et al. 2013; Polito et al. 2017).

Conclusions

Here, I offer several insights into Hutton's shearwater dietary and sexual segregation during the breeding and non-breeding period. First, the isotopic composition of induced Hutton's shearwater tail feathers did not conform with the potential prey species composition, and therefore I suggest that either the birds are foraging on something I did not sample or they are foraging in areas outside of the Kaikōura near-shore environment. A possible foraging area may be within the Banks Peninsula offshore region as isotopic composition of zooplankton were consistent with the isotopic composition of induced shearwater feathers. Second, fractionation models applied to the Kaikōura near-shore plankton and fish samples did not explain the observed isotopic composition and may not apply to these particular birds. Third, there was a significant difference between the non-breeding and breeding seasons as the food chain contained different isotopic bulk $\delta^{13}C$ and $\delta^{15}N$ composition. Finally,

there was a significant difference in stable isotopic composition between the males and females during the non-breeding period, but not during the breeding season. I believe that spatial and temporal segregation between the sexes would be the most parsimonious explanation for the results I observed. This study has started to provide the necessary background knowledge and understanding of the Hutton's shearwater foraging behaviour through stable isotope analysis. The sexual, spatial and temporal patterns in foraging behaviour that I recorded will aid in the development of future conservation management strategies.

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Adult male Hutton's shearwater equipped with GPS tracker before leave from the Kaikōura Peninsula colony launch pad, 10 January 2017 (photo by DG Bennet).

Chapter 4

Fly south: foraging locations of the Hutton's shearwater (*Puffinus huttoni*) revealed by GPS tracking

Abstract

The Hutton's shearwater *Puffinus huttoni* is endemic to Kaikōura, New Zealand, but the spatial and temporal aspects of its at sea foraging behaviour are not well known. To identify foraging areas, determine diving depths, and estimate trip durations, I deployed GPS devices and Time-Depth Recorders on 23 adult Hutton's shearwaters during the chick-rearing period in 2017. I found shearwaters travelled from their breeding grounds at Kaikōura to coastal and oceanic areas situated 125–325 km south and near Banks Peninsula. Trip durations varied from 2 to 15 days (mean = 6), while dive depths ranged from 3 to 16 m (mean = 5.5 m). However, flight paths and durations varied between individuals, and it is not clear whether the patterns I observed were affected by recent earthquakes in the area, or by other fluctuations in the environment. Mapping the spatial and temporal distribution of Hutton's shearwaters at sea will be fundamental to their conservation; as such information can reveal potential areas of conflict with fisheries and other industrial users of the marine environment.

Introduction

Seabirds are important to the marine ecosystem and can be used as indicators of environmental health (Furness & Camphuysen 1997; Piatt et al. 2007), but they are also one of the most threatened groups of marine species (Croxall et al. 2012). Whether used as environmental indicators (e.g., pollution), inferring fish stock abundance (e.g., predator-prey relationship), or as indicators of climate change and anthropogenic effects (e.g., fisheries by-catch), seabirds are also useful barometers for setting conservation actions (Thompson & Hamer 2000; Smithers et al. 2003; Piatt et al. 2007; Dias et al. 2011; Grémillet et al. 2014; Brisson-Curadeau et al. 2017; Ponchon et al. 2017). As anthropogenic activities increase, conflicts between marine species and tourism, fisheries, and deep-sea oil exploration are also increasing (Piatt et al. 1990; Uruski 2010; Markowitz et al. 2011; Velando & Munilla 2011; Richard et al. 2015). Thus, it is important to understand the complex relationships between seabirds and human activities, and how to manage these conflicts.

Methods for monitoring seabirds within their breeding colony (e.g., breeding success) are well established (Weimerskirch & Cherel 1998; Phillips 2006; Neves et al. 2012), but the marine environment can be inaccessible to researchers, and therefore studies of the at sea behaviour of seabirds are under-represented in the literature (Spear et al. 2007). With the recent improvement in accuracy, reduction in size and weight of Global Positioning Systems (GPS), and Time-Depth Recorders (TDR), it is now possible to track smaller species, making the at sea behaviours more practical for research (Freeman et al. 2010; Navarro et al. 2013). Mapping the movements of birds at sea is a key first step in understanding the impacts of human activity on threatened

species, aiding in the establishment of marine protection areas (MPAs) and to enhancing our knowledge of seabird-fisheries interactions (Croxall et al. 2012).

During the breeding season, most seabirds are central place foragers, returning regularly to breeding colonies to incubate or feed their chick. While at sea, some species are known to travel over large distances to reach profitable foraging sites (Dell'ariccia et al. 2010; Jodice & Suryan 2010). The quality of local productivity and foraging conditions can greatly influence the foraging behaviour of a species, whereby some individuals may either forage at great distances from the colony or remain close to the nesting site (Jaeger et al. 2014; Matsumoto et al. 2017; Paiva et al. 2017). Such 'bimodal' patterns of distribution at sea have been found in some species, such as Cory's shearwater *Calonectris diomedea*, sooty shearwater *Puffinus griseus* and wandering albatross *Diomedea exulans* (Weimerskirch et al. 1997; Shaffer et al. 2009; Paiva et al. 2010b; Paiva et al. 2017). However, patterns of foraging can change due to seasonal changes in environmental conditions (e.g., chlorophyll *a* levels), increased levels of competition, stochastic events (e.g., seismic events), and greater anthropogenic pressures (e.g., fisheries) (Jodice & Suryan 2010; Alonso et al. 2012; Richard et al. 2015; Paiva et al. 2017). As commercial fisheries typically exploit the same highly productive areas as seabirds (Ballance et al. 1997; Taylor 2000; Catry et al. 2009; Neves et al. 2012), some species can become casualties of by-catch (Richard et al. 2015).

New Zealand has more than double the number of threatened seabird species than any other country, of which 33 are endemic (Croxall et al. 2012). Pelagic seabirds are especially threatened, as they are more likely to decline than coastal seabirds (Croxall

et al. 2012). While population decline is often attributed to on-land predation (e.g., cats, rats, stoats, foxes, mice, and pigs) (Croxall et al. 2012; Wanless et al. 2012; Medina et al. 2014), little is known about the at sea foraging behaviour and risks seabirds face in the marine environment. The Hutton's shearwater *Puffinus huttoni* is a breeding seabird endemic to the Kaikōura region of New Zealand. Although its breeding biology has been well studied, most observations of its at sea behaviour are anecdotal (see Chapter 3) (Taylor 2000). For example, flocks of Hutton's shearwater have been reported within the Cook Strait, along the Kaikōura and Canterbury coastline to Banks Peninsula and out to the Chatham Rise (Harrow 1976; Hawke 1998; Pinkerton 2011). Residents of Kaikōura have also reported 20,000 Hutton's shearwaters foraging on small unidentified fish in September 1967 (Harrow 1976), but more often these flocks contain around 50–500 individuals or less (Marchant & Higgins 1990). A more systematic assessment of at sea activities may help us to understand more about the Hutton's shearwater foraging ecology, how susceptible they are to anthropogenic activity, and how they may be affected by shifts in the ocean conditions (Taylor 2000; Cuthbert 2001).

The objectives of this study were to: (1) describe the behaviour of Hutton's shearwater while they are at sea through the deployment of miniaturised GPS and TDR technology, and (2) identify the flight paths, foraging areas and direction of travel during the chick-rearing period. I compared foraging areas and habitat use through spatial and temporal distribution of individuals, estimates of diving depths and duration of foraging trips. I used diving depth and duration as indicators of foraging locations. I also compared chlorophyll *a* concentration and bathymetry to assess foraging behaviour of the species. My data provides a baseline in mapping the

spatial and temporal distribution of Hutton's shearwaters at sea, which will be fundamental to their conservation, and for mitigation of conflict with fisheries and other industrial users of the marine environment.

Methods

Ethical statement

This study was performed with permission of the New Zealand Department of Conservation (WAA-38708-FAU) and the University of Canterbury Animal Ethics Committee (2014/20R Amendment 2).

GPS and TDR deployment

During January 2017, breeding Hutton's shearwater adults were captured from their nesting burrows within the recently established Kaikōura Peninsula colony (Te Rae o Atiu; –42.4286 S, 173.7029 E). Eight PinPoint50 Global Positioning System trackers (GPS; 22 x 13 x 9 mm, 2.2 g, Lotek Wireless), five Uria100 GPS trackers (35 x 16 x 11 mm, 8.5 g, Ecotone) and eight LAT1500 Time-Depth Recorders (TDR; 8 × 32 mm, 3.4 g, 512 Kb memory, Lotek Wireless) were deployed on 23 birds during the chick-rearing period. All twelve nests that contained a chick were instrumented with both adults being tracked, except one nest in which only one adult was used. Only one adult from each pair was tracked at a time and redeployment on the nesting partner was not initiated until 1–2 days later. All birds had been banded and sexed previously, and individual identification was confirmed through the leg band number.

To fit the tracking equipment, birds were caught by hand from within the artificial nesting boxes provided. The GPS tracker and TDR logger were prepared and software programmes deployed before attaching to an individual. Birds were held within a black cotton bag to reduce stress and prevent biting. While bagged, adults were weighed prior to equipment attachment and after retrieval using a spring Pesola balance (± 5 g).

To avoid irritation from a chest harness, and to avoid restriction and disruption to wing loading, tape was used to attached GPS trackers (Warham 1990; Falk & Møller 1995; Nicholls et al. 2002; Phillips et al. 2003). GPS trackers (both models) were attached to a small group of feathers between the shoulders using TESA tape (Guilford et al. 2008). Each device was positioned directly above the centre of gravity of the bird. Four thin strips of TESA tape were placed under four small sections of feathers (7 x 1 cm tape length), and the GPS tracker was aligned with the antenna directed down the spine. The end of the tape was then folded over the tracker and secured. After securing, any twisted or trapped feathers were repositioned. The combined weight of the Uria100 GPS attachment with tape (10 g, 2.86 %) was within 3 % of a bird's body weight (~350 g) (Warham 1977; Cuthbert 2001). The Uria100 were initially set to collect data at 5-minute intervals which then increased to 15-minutes, whereas the PinPoint50 GPS trackers were set at 10-min, 30-min and 60-min intervals. This progression in collection time assisted in recording as many return foraging trips as possible.

TDR loggers were secured to a plastic leg band on the left tarsometatarsus, with the pressure sensor facing towards the foot to limit potential effects of acceleration

(Elliott et al. 2008). The TDR loggers recorded pressure (resolution 0.05 %), internal device temperature (resolution $>0.05^0$ C), and wet/dry state at 5-second intervals. TDR loggers were deployed in combination with the PinPoint50 GPS units. The combined weight and attachment (7.7 g, 2.2 %) of each logger combination was within 3 % of a bird's body weight (~350 g) (Warham 1977; Cuthbert 2001). Before deployment, each chick was weighed and if over 175 g, an adult was then equipped with recording equipment. Logger deployments were completed between 22:00–04:30 h.

After fitting the TDRs and GPSs, birds were recaptured to recover, download and redeploy each logger. All recaptures and retrievals of loggers were carried out from 23:30–04:15 h. Each nest entrance was marked with vertical pegs indicating the arrival and departure of a bird and each nest was checked on average every 15 minutes (10–20 min). Nests were monitored nightly from approximately 22:00 to 05:00 h, unless prevented by severe weather. When birds arrived back at the colony, time was allowed for adults to provision chicks, to prevent food loss due to human disturbance. During capture, birds were examined for signs of damage caused by the TDR units; none was recorded. The TESA tape was peeled off the GPS tracker and removed from the feathers. Few feathers were lost, and no damage or tape residue was detected on the remaining feathers. The TDR logger zip-tie was cut with scissors, the leg was checked, and no skin abrasion was observed. All birds were released back into their burrows, and the entrance covered for a few minutes to allow the bird to resettle with its chick. A foraging trip was defined as beginning with the departure from the colony and ended at the first return to the nest.

Data Analysis

All TDR data files were downloaded (Lotek, Tag Talk, Canada) and processed through the program MultiTrace-Dive (Jensen Software Systems, Germany; version 2014.5.0.0). Dive depth analysis was set to 'when wet and ≥ 1.5 m' to remove TDR manufacturing error (1 % error over 100 m = 1.0 m error) and barometric pressure influence on the top 0.5 m of water.

All GPS files were downloaded using preparatory software. I used a remote radio link data transmission system to download the Uria100 data. The base station was installed in the colony and automatically acquired the flight information each time a bird came within range of the base station (up to 500 m). PinPoint50 data was transferred directly to the computer after retrieval from the bird by cable connection.

I tracked 11 foraging trips and recorded TDR activity from five individuals during the 23 deployments (11–27 January 2017; Table 4.1). Six tracks were collected from three Uria100 GPS units (one unit was deployed twice and another three times) and five tracks from three PinPoint50 GPS units (two units deployed twice and the third unit was deployed three times). One bird was not recaptured on initial return and subsequently completed a second foraging trip before the unit was retrieved; only the first GPS track has been used for analysis. Unfortunately, two PinPoint50 GPS trackers returned waterlogged, and seven GPS units were lost at sea (birds returned to colony without the units). Two birds failed to return to the colony within my time at the colony.

Table 4.1 Summary of deployments of GPS and TDR data loggers attached to Hutton's shearwaters adults in the Kaikōura Peninsula colony during the breeding season in 2017. Y: bird returned to the colony with a continuous GPS track, N: GPS tracker battery depleted prior to returning to the colony. U100: Uria100, Ecotone GPS tracker; PP50: PinPoint 50, Lotek Wireless GPS tracker.

Bird	Nest	Band	Sex	TDR	GPS		Date		Trip	
					Style	Fix Rate (min)	Deployment	Recovery	Length (d)	Completion
A	N42	X16908	Female		U100	5	11 Jan	20 Jan	9	N
B	N77	X16926	Female		U100	5	11 Jan	13 Jan	2	Y
C	N45	X16963	Female	Y	PP50	10	11 Jan	13 Jan	2	N
D	N37	X19665	Male	Y	PP50	10	11 Jan	16 Jan	5	N
E	N40	X17261	Male		U100	5	12 Jan	20 Jan	8	N
F	N53	X17334	Male	Y	PP50	30	15 Jan	24 Jan	9	N
G	N90	X17105	Female		U100	5	16 Jan	20 Jan	4	N
H	N40	X17000	Female		U100	15	21 Jan	25 Jan	4	Y
I	N37	X16995	Female		U100	15	26 Jan	25 Jan	2	Y
J	N42	X16980	Male	Y	PP50	60	26 Jan	28 Jan	2	Y
K	N51	X17216	Male	Y	PP50	60	26 Jan	10 Feb	15	N

Four GPS units recorded the return journey of three males and one female over a period of two to four days. Seven foraging trips were incomplete due to battery depletion and were only used to map the outward-bound flight direction, and maximum distance travelled from the colony by each bird. Maximum distance travelled was calculated from four individuals with complete return journeys (range 2–4 days). A fifth individual was on a return journey, but the GPS battery depleted 7.5 h before retrieval and was not included in the completed journey data set.

TDR dive depth and duration data recorded within 15 minutes of a GPS location (PinPoint50, data collection rate 10–60 min) were used to indicate foraging locations. GPS dive durations (pre-set range 10–60 s) recorded within 15 min of a GPS fix and flight speeds (speed ≤10 km h^{-1}) recorded by the Uria100 GPS units were also used to indicate potential foraging sites. GPS speeds ≤10 km h^{-1} were classed as either foraging, birds taking off, or landing, or resting on the water surface (Weimerskirch et al. 2006; Kotzerka et al. 2010; Paiva et al. 2010a). The associated Uria100 GPS coordinates and applied equipment limits were used to generate kernel density maps (probability level of 95%), allowing me to identify core areas used during foraging trips (day 05:00–22:00 h and night rafting 22:01–04:59 h). The night rafting behaviour was assessed at a 15 min GPS fix rate, whereas the dive duration day rate encompassed 5–15 min fixes.

Dive depth and dive duration were tested for normality (Shapiro-Wilk test) and homoscedasticity (Levene's test). As the assumptions of parametric tests were not met, data were analysed by Kruskal-Wallis tests (R version 3.3.0). TukeyHSD was used to show where differences existed between samples. Chlorophyll *a* concentration

and bathymetry were tested with a one-sample t-test and compared to the calculated population mean of the three known foraging sites (combined). Changes in body mass during foraging trips were analysed using Wilcoxon signed-rank test (package 'coin' version 1.1-3). Differences related to sex and weight were tested using the Mann-Whitney U test. Unless otherwise stated, all values are presented as predicted 95% confidence intervals.

Graphs were produced by Grapher12 (12.5.811). The chlorophyll *a* map, in mg m^{-3} concentration (approximately 4 x 4 km; 0.04^0 spatial resolution), was downloaded as a GeoTIFF raster from Aqua MODIS covering a period of one month (1 January-1 February 2017; 'https://neo.sci.gsfc.nasa.gov'), and the New Zealand Bathymetric map was downloaded from ArcMap 10.4 (World Oceans Base Map). Chlorophyll *a* and bathymetric data (NOAA GEBCO; 1-minute bin spaces) were downloaded from NEO NASA Earth Observation as CSV files ('https://neo.sci.gsfc.nasa.gov') for analysis.

Results

Birds weighed on average 344.1 ± 19.8 g (n = 11, range 315–435 g) before equipment deployment and between 310–400 g with an average weight of 328.2 ± 11.8 g at retrieval. This difference was non-significant (Wilcoxon signed-ranks test: W = 40, Z = 1.29, P = 0.22, r = 0.39). The weight variation between deployment and return ranged from +105 to –35 g, with no differences between sexes (Mann-Whitney: U = 21, n_{female} = 6, n_{male} = 5, P = 0.32). All chicks successfully fledged from nests in which at least one adult was fitted with a device.

Distribution and direction of foraging trips

GPS tracks were plotted to show the distribution of foraging movements during the chick-rearing period (Fig. 4.1). Outward-bound flight paths for nine individuals were towards the southwest and tracked the coastline, but one bird from this group changed direction and headed southeast after approximately 40 km. Two birds left the colony and flew southeast over oceanic waters. This pattern was further evident by plotting the location of each bird during the first 24-hour period of flight movement (latitude and longitude) against time (Fig. 4.2). All birds consistently moved south from the colony (Fig. 4.2a). During the same timeframe, movement in longitude was variable (Fig. 4.2b) but most birds were observed initially flying west (i.e., tracking the east coast of the South Island), and then veering east.

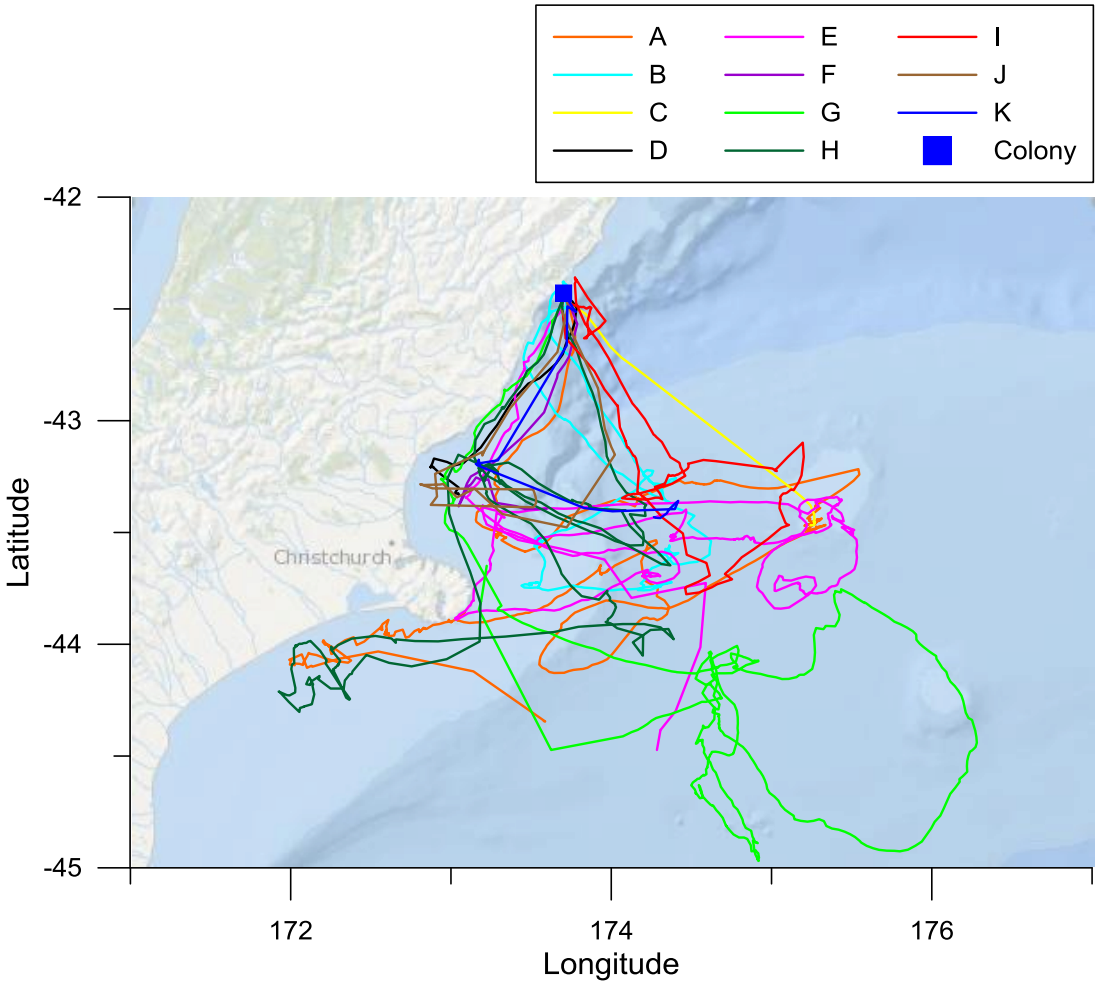

Figure 4.1 Plot of all fixes for each GPS tracked Hutton's shearwaters during the chick-rearing period (11–27 January 2017). Different colours used to indicate each bird. Complete return tracks for birds B, H, I, and J. Partial foraging trips recorded for birds A, C, D, E, F, G, and K. Kaikōura Peninsula colony location indicated by a solid blue square.

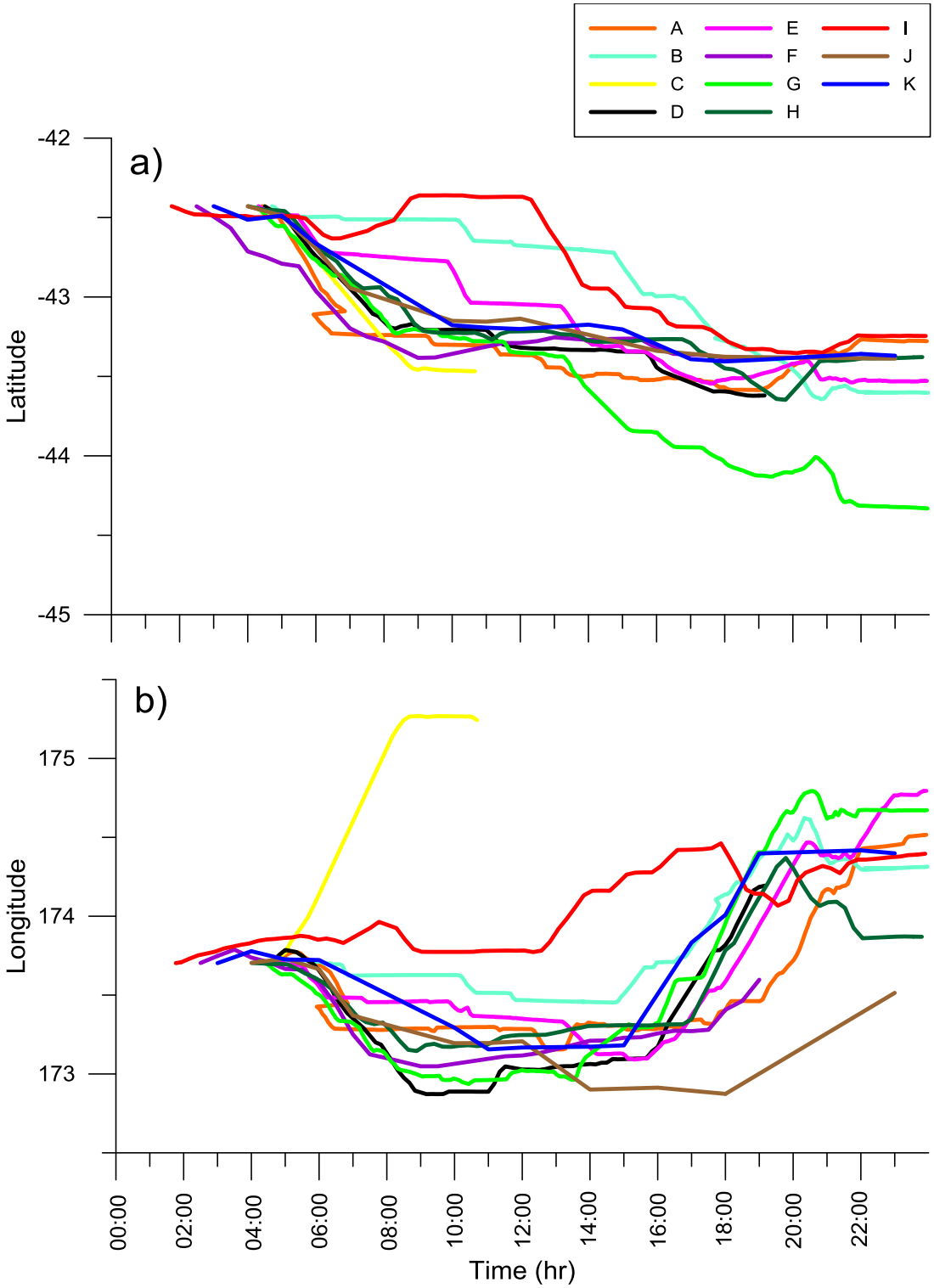

Figure 4.2 Plot of all outward-bound tracks recorded over the first 24-hours, independent of date. a) Latitude by time and b) longitude by time for 11 Hutton's shearwaters departing the colony and heading south. Individual colours used to indicate each bird.

Kaikōura near-shore behaviour

Although the tracks shown in figure 1 indicate that birds ultimately flew to destinations well away from the breeding colony, a few areas were identified where birds spent time at the beginning of their foraging trip within the coastal Kaikōura waters (Fig. 4.3; Uria100 GPS). Three individuals spent time within 30 km of the peninsula before flying south: (1) Bird E: 2 h on 12 January 2017 within 9 km, 04:26–06:28 h; (2) Bird B: 5 h on 12 January 2017 within 12 km, 05:03–10:12 h; and (3) Bird I: 10 h on 26 January 2017 within 25km, 02:11–12:19 h. Diving events were recorded for two of these birds, with an average dive duration of 27.3 ± 5.5 s (n = 34; range = 10–60 s). Although Bird I spent the longest period of time in proximity to Kaikōura, no dives were detected.

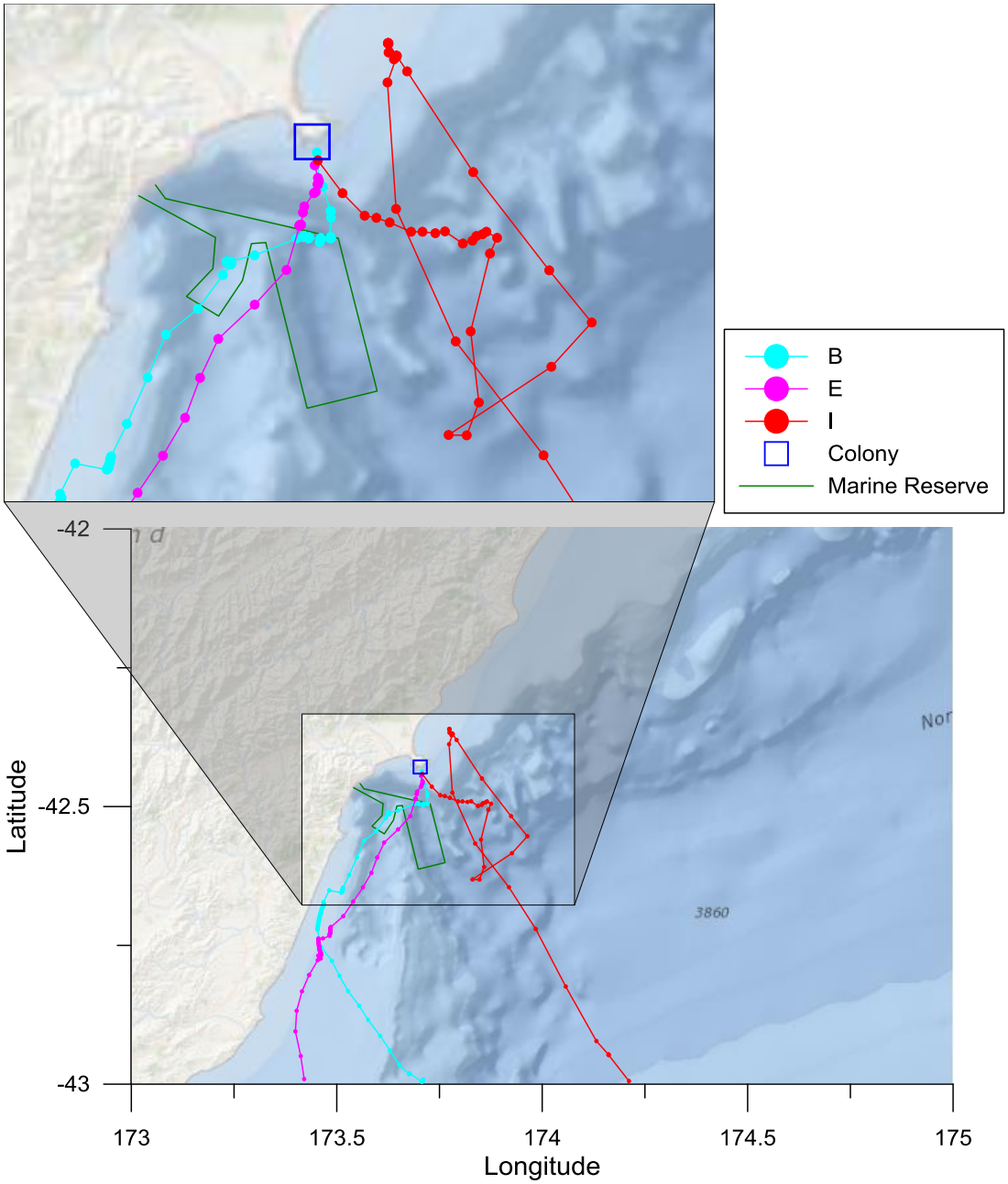

Figure 4.3 Plot of fix locations (circles) and flight tracks for three outbound birds that spent time within 30 km (zoomed box) of the Kaikōura Peninsula colony during the chick-rearing period (11–27 January 2017). Individual colours used to indicate each bird. The Kaikōura Peninsula colony (hollow blue square) and the Hikurangi Marine Reserve (green line) locations are indicated within the zoomed area.

Trip duration and distance from colony

The average distance from the colony to the furthest point travelled during a completed foraging trip was 173 km (range 125–247 km; Fig. 4.4), and the average total track length was 1020.25 km (range 457–1613 km). However, the furthest distance recorded for a bird was 326 km, although this was obtained from battery-depleted GPS unit and it is possible the bird may have flown even further. The furthest point recorded east of Banks Peninsula was approximately 260 km. For all birds returning with GPS trackers still attached, the at sea foraging trip ranged between two and 15 days (6 ± 2.5 d). I found no clear evidence of a bimodal foraging pattern within the Hutton's shearwater GPS data, although the small sample size limited the ability to detect such a pattern.

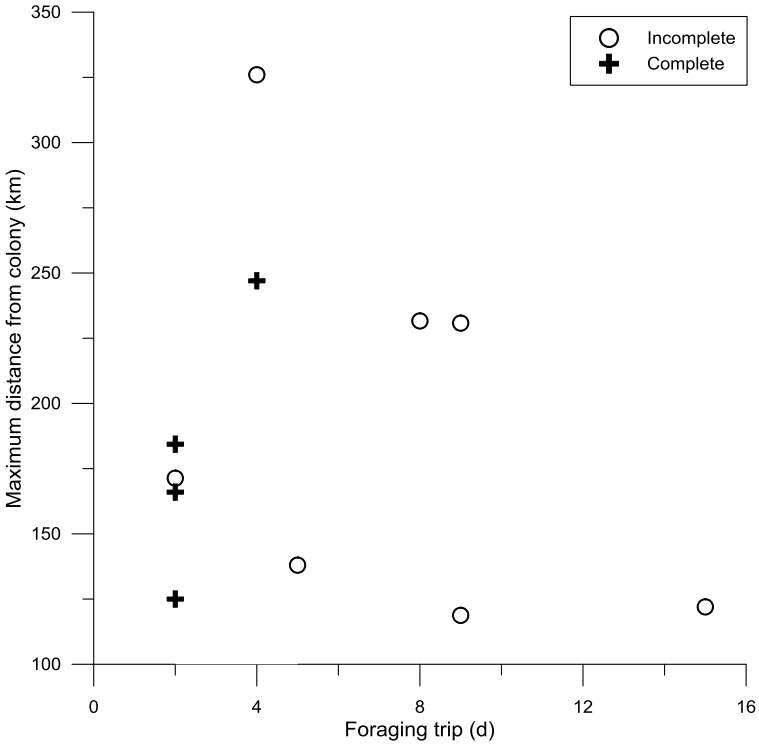

Figure 4.4 Maximum foraging distances (km) for all recorded foraging trips from the Kaikōura Peninsula in 2017, in relation to duration (d) of foraging trip at sea. Symbols indicate incomplete and complete GPS fixes for the return of foraging trips.

It might be expected that birds away from the colony for the longest period also flew the furthest. I tested the relationship between the maximum distance from the colony and the length of the foraging trip (Fig. 4.4). There was no statistical relationship detected (r_9= -0.19, n = 11, P = 0.58).

Return journey

Of the 11 tracked birds, four individuals (three males and one female) completed a return journey over a period of two to four days (1x PinPoint50, 3x Uria100; Fig. 4.5). After approximately 48-hours at sea, three individuals started their return trip towards the colony by heading north around 20:00–21:00 h (Fig. 4.6a) and with little

longitudinal variation during the return trip journey (Fig. 4.6b). The fourth individual remained at sea for a further 48-hours before completing the return trip.

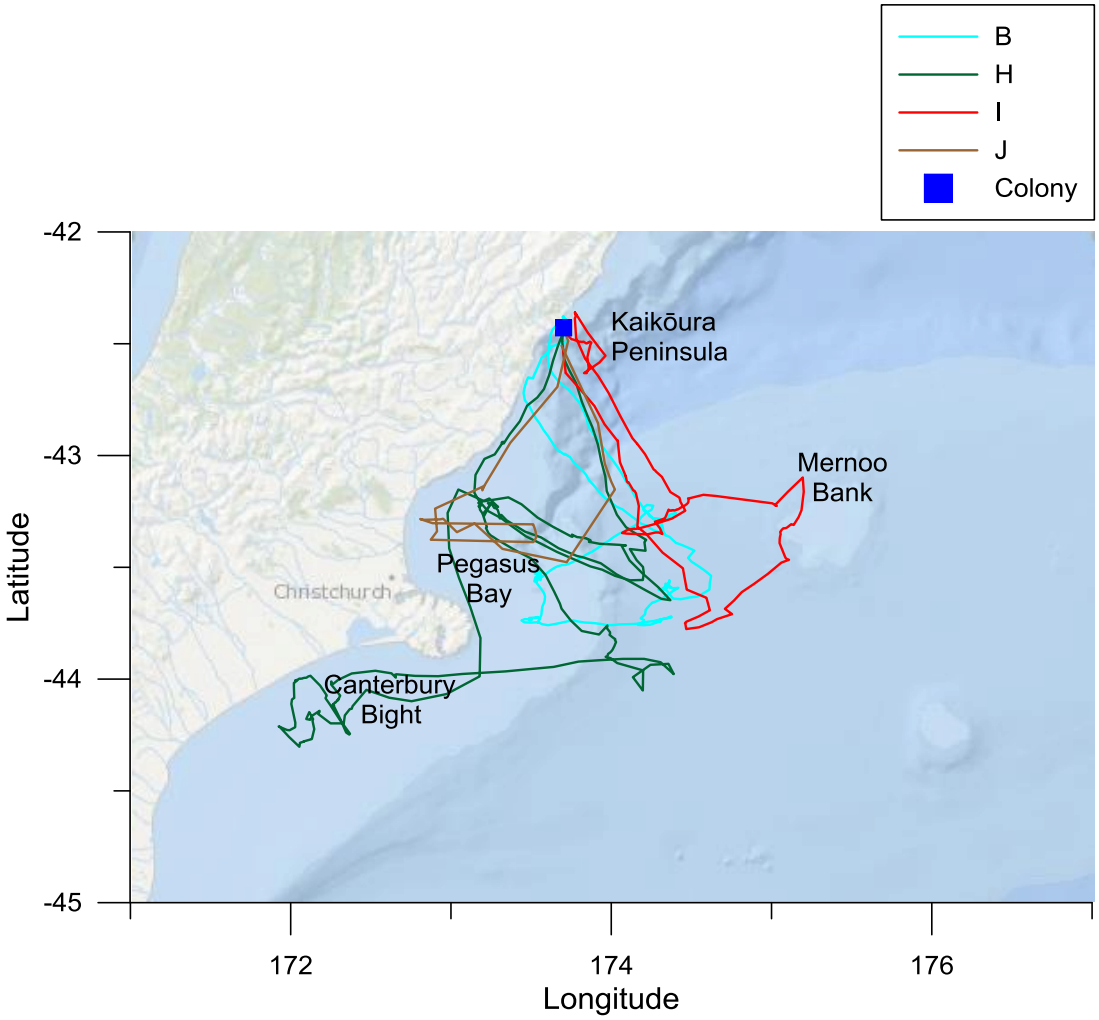

Figure 4.5 Plot of all fixes for each GPS tracked birds that completed a return journey during the chick-rearing period (11–27 January 2017). Individual colours used to indicate each bird. Kaikōura Peninsula colony location indicated by a solid blue square.

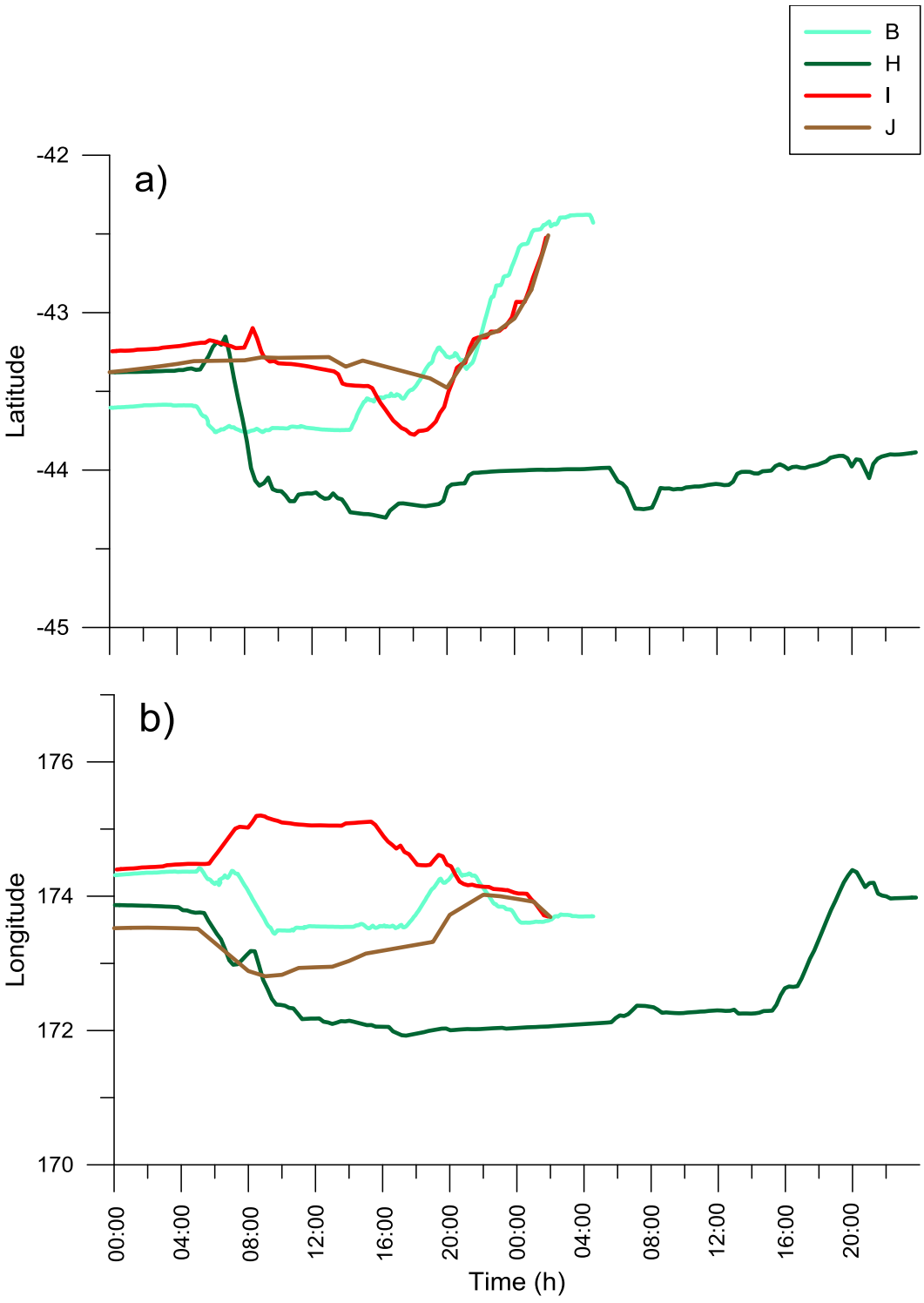

Figure 4.6 Plot of tracks recorded over a 48-hour period during the second and third day at sea for birds that completed a foraging trip, independent of date. a) Latitude by time and b) longitude by time for four Hutton's shearwaters adults foraging at a distance from the colony and the return tracks for three individuals. The fourth bird remained at sea for a further 24 hours. Individual colours used to indicate each bird.

Foraging locations

Numerous potential foraging sites were identified by plotting the locations of dives, using GPS dive duration and flight speeds (Fig. 4.7) and TDR dive depths (Fig. 4.8) recorded within 15 min of a GPS fix (during the hours of 05:00–22:00). Foraging locations were concentrated to the south and southeast of the colony (Figs. 4.7 & 4.8). Three main clusters were identified, two coastal (Pegasus Bay and Canterbury Bight) and one over the Mernoo Bank. The average dive duration recorded when the range limits were set (≤10 km h^{-1}) was 22.2 ± 0.4 s (n = 2689).

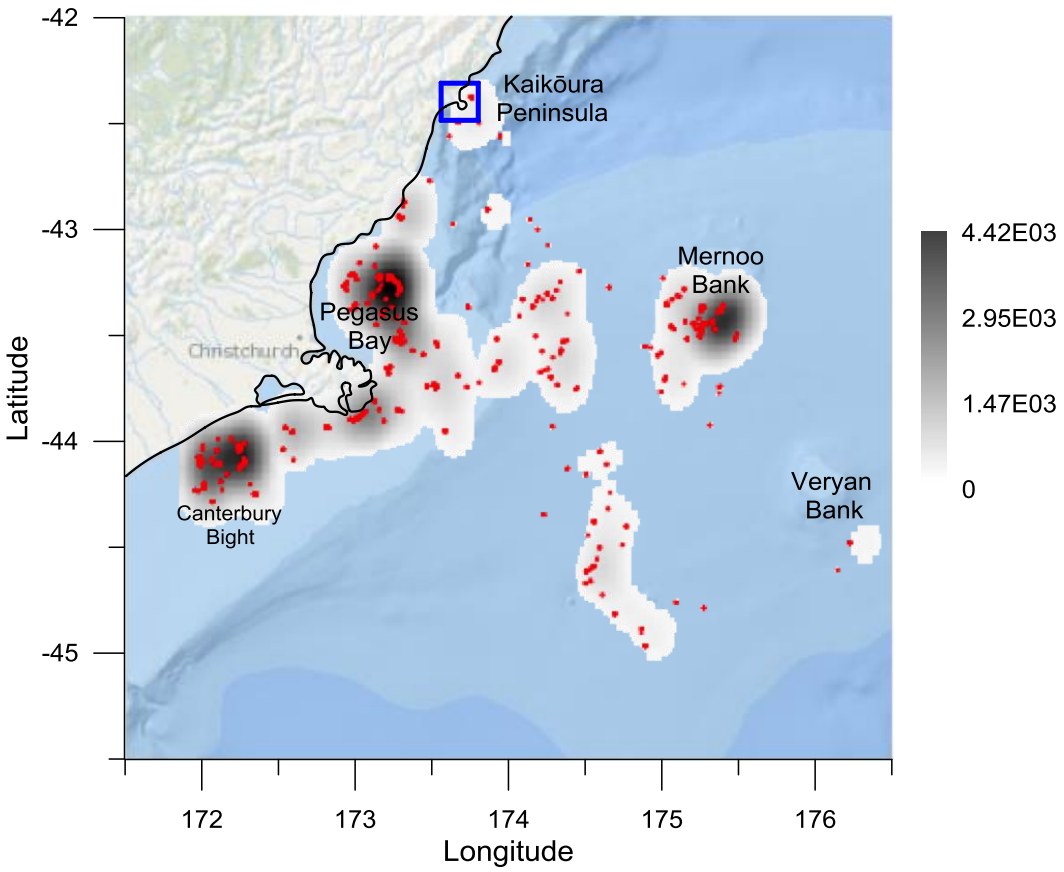

Figure 4.7 Kernel density plot of diving locations by Hutton's shearwaters. Greyscale indicates the probability distribution of a bird being in an area (black = high, white = not present; grid 4 km resolution). Red dots indicate GPS fixes and locations overlaid on a coastal map. Kaikōura colony location indicated by a blue square. Diving was defined by birds that were recorded as travelling at speeds <10 km h^{-1}.

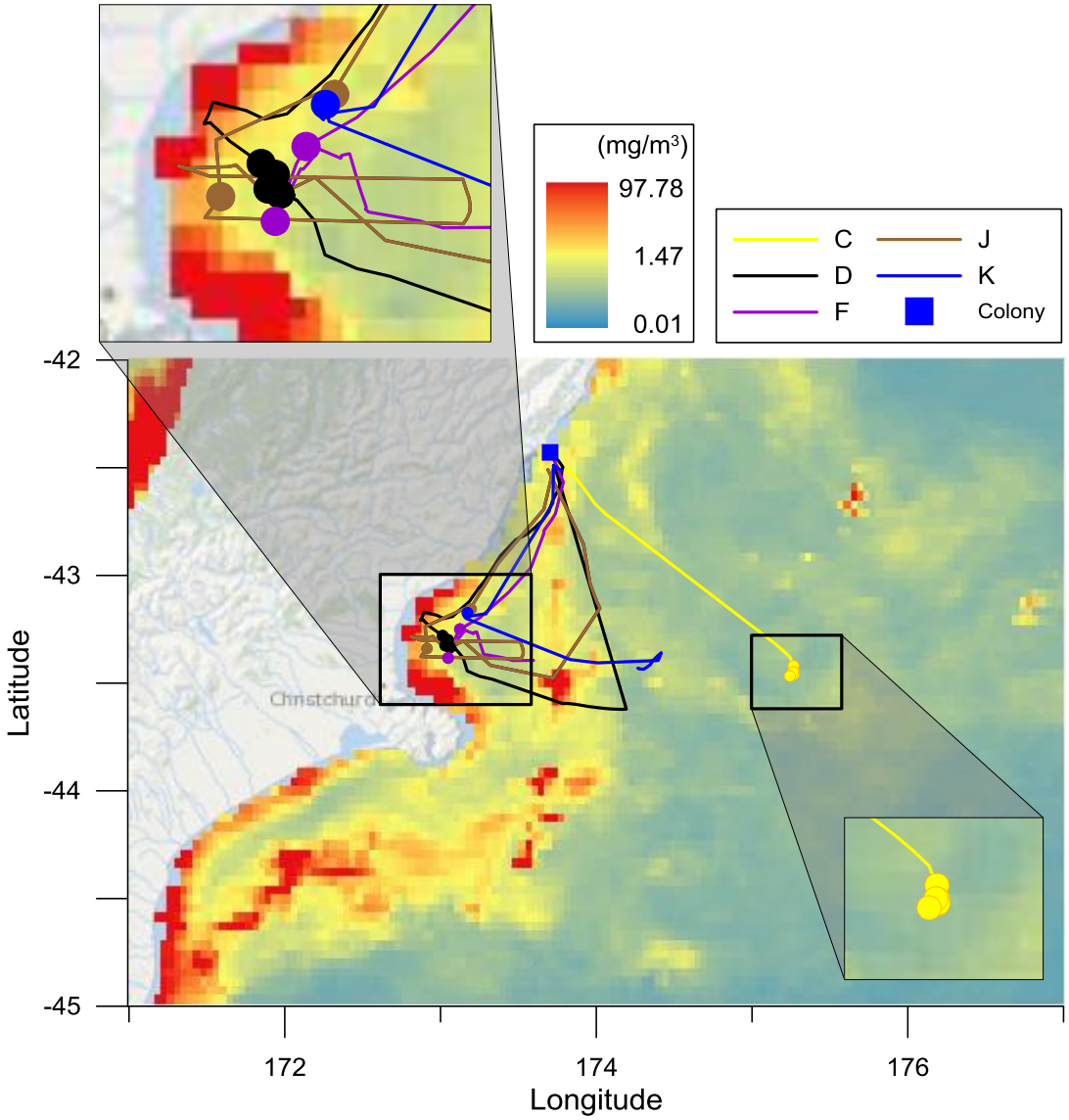

Figure 4.8 Plot of GPS fixes for corresponding diving locations for each TDR tracked bird during the chick-rearing period (11–27 January 2017). Individual colours used to indicate each bird overlaid on a chlorophyll *a* concentration map (1-month resolution). Coloured dots indicate TDR diving locations for each individual (Bird C and D on 11 January, bird F on 15 January, and birds J and K on 26 January 2017). Colour scale indicates the chlorophyll *a* concentration in an area at a 4 km resolution (red = high, blue = low).

When the flight speed was set at ≤10 km h^{-1}, the average speed of a bird was 1.9 ± 0.2 km h^{-1} (n = 550) indicating foraging, resting, landing or take-off behaviour. In contrast, when all flight speeds were analysed (including above behaviours and

commuting between locations), the average flight speed of 10.7 ± 0.4 km h^{-1} was recorded for tracked birds (n = 3784; range = 0–52 km h^{-1}).

A total of 63 dive events were recorded from five TDR equipped birds (11 January 2017, four male and one female; Fig. 4.8) over an 8.5 h period (07:30–16:00 h). The maximum depth reached was 16.4 m, and an average maximum depth was 9.2 ± 5.6 m (n = 5 individuals). The average diving depth was 5.5 ± 0.9 m (n = 63 dives). The maximum and average maximum dive durations recorded were 45.0 s and 24.9 ± 10.2 s (n = 63), respectively. The average diving duration was 17.4 ± 2.2 s (n = 63 dives; range = 8.3–45 s).

For individuals with more than 10 TDR dive events (n = 3 individuals), I assessed diving depth and duration within the Pegasus Bay (coastal) and Mernoo Bank (oceanic) regions. Although sample sizes are small, I found a significant difference between the diving depths (Kruskal Wallis: $H_{3, 56}$ = 10.43, P < 0.001) and duration (Kruskal Wallis: $H_{3, 56}$ = 15.74, P < 0.001). A significant variation in diving depth was seen between Bird D (oceanic) and Bird C (coastal) (TukeyHDS P < 0.001), but not Bird D-Bird F (coastal) or between the coastal birds F-C (TukeyHDS P = 0.99, P = 0.18; respectively). Dive duration varied significantly between Birds D-C and D-F (TukeyHDS P < 0.001, P = 0.01; respectively), but no variation was seen for Birds C-F (TukeyHDS P = 0.23).

Chlorophyll a and bathymetry

To determine if Hutton's shearwaters were foraging in areas likely to be of high productivity, I compared chlorophyll *a* concentration levels (1 January-1 February

2017) and bathymetry among four locations (Table 4.2). Three areas were identified as foraging locations of the Hutton's shearwater from the GPS and TDR results. Figure 8 illustrates the TDR dive records plotted against chlorophyll *a* (1 January-1 February 2017; 1-month resolution) as a visual representation. The fourth location was situated south of the Kaikōura Peninsula colony where birds have been observed rafting and it was believed that this area was a main foraging site of the Hutton's shearwater. This selected location also includes the Kaikōura Marine Protection Area (MPA) (Fig. 4.9). I found a significant difference in bathymetry ($t = 4.504$, d.f. = 18, $P < 0.01$) between the combined foraging sites (mean = 74.08 m, $n = 74$) and the non-foraging site (mean = 528.80 m, $n = 19$), but no difference was found in chlorophyll *a* concentration ($t = 0.165$, d.f. = 15, $P = 0.87$) between the foraging sites (mean = 1.28 mg m^{-3}, $n = 75$) and the non-foraging site (mean = 1.29 mg m^{-3}, $n = 16$).

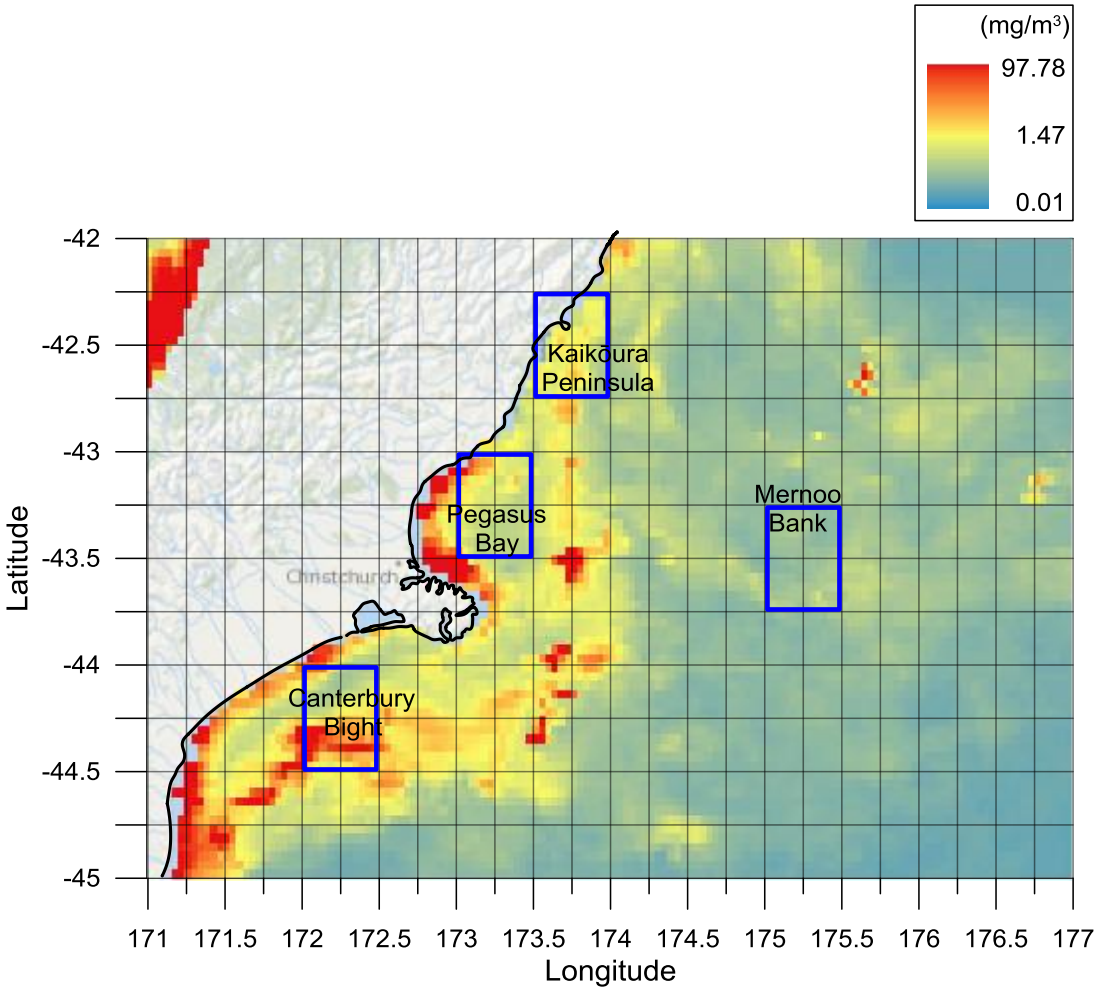

Figure 4.9 Grid map indicating the areas from which chlorophyll *a* and bathymetric data were selected for analysis. Each box indicates an area of 0.5 x 0.5 degree of latitude and longitude for the Kaikōura Peninsula area, Pegasus Bay, Mernoo Bank and the Canterbury Bight. Colour scale indicates the chlorophyll *a* concentration in an area at a 4 km resolution (red = high, blue = low).

Table 4.2 Summary of chlorophyll *a* values (mean ± CI) and bathymetry (mean ± CI) for areas utilised by Hutton's shearwater adults during 2017 breeding season.

			Chlorophyll *a* (mg m^{-3})			Bathymetry (m)		
Area	Latitude	Longitude	*n*	Mean ± CI	Range	*n*	Mean ± CI	Range
Canterbury Bight	–44.00 to –44.50	172.0 to 172.5	25	1.59 ± 0.49	0.86 – 2.44	25	37.8 ± 11.55	0 – 95
Mernoo Bank	–43.25 to –43.75	175.0 to 175.5	25	0.73 ± 0.08	0.61 – 0.94	25	149.92 ± 29.23	32 – 315
Pegasus Bay	–43.00 to –43.50	173.0 to 173.5	25	1.52 ± 0.60	0.96 – 3.48	24	32.81 ± 14.38	0 – 126
Kaikōura Peninsula	–42.25 to –42.75	173.5 to 174.0	16	1.29 ± 0.21	0.89 – 1.68	19	528.80 ± 262.32	0 – 1780

Nocturnal behaviour

Night-time rafting locations were identified for birds with a GPS fix rate set at 15 min and flight speeds ≤10 km h^{-1} (Fig. 4.10). An average flight speed of 1.3 ± 0.1 km h^{-1} (n = 378; range 0–8.8 km h^{-1}) was recorded between 22:01–04:59 h and I found one individual with rafting behaviour in the evening near the Kaikōura Peninsula (Bird B, see below). Night-time rafting behaviour was identified near the Mernoo Bank area, within Canterbury Bight and toward Banks Peninsula. Water depth ranged from ~40 m for coastal waters (Table 4.2) to >1000 m deep oceanic waters. Bird I was identified as remaining off the coast of the Kaikōura Peninsula during the early hours of the morning (2:26–4:57 h) before commencing diving activity (1.7 ± 0.5 km h^{-1}, n = 10; range 0.9–3.6 km h^{-1}) but only one individual was identified during the return journey. Bird B was found with an average speed of 1.3 ± 0.4 km h^{-1} (n = 13; range 0.3–3.0 km h^{-1}) within 15 km of the colony and spent time offshore of the Kaikōura Peninsula before returning to the nest site (0:21–4:28 h).

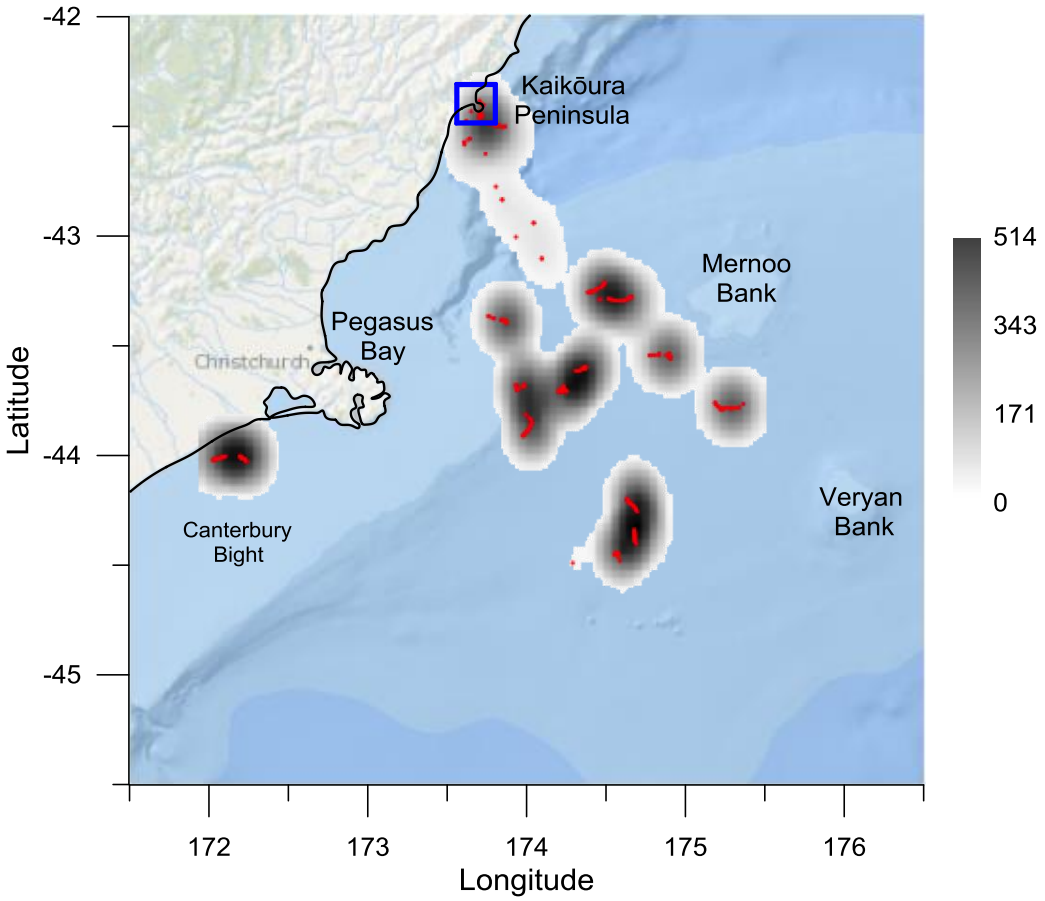

Figure 4.10 Kernel density plot of all locations where birds were travelling at speeds <10km h^{-1} rafting at night (22:01–04:59 h; 15 min fix rate) were classed as rafting locations (Uria 100 GPS, $n = 6$). Greyscale indicates the probability distribution of a bird being in an area (black = high, white = not present; grid 4 km resolution). Red dots indicate GPS fixes and locations overlaid on a coastal map. Colony location indicated by a blue square.

Discussion

My results provide some of the first detailed information on the tracking and foraging behaviour of the New Zealand endemic Hutton's shearwater during the chick-rearing period. My results demonstrate that Hutton's shearwaters leave the Kaikōura Peninsula colony to forage at distances up to 326 km and remain at sea for up to 15 days before returning to the colony. Few birds spent time within the coastal Kaikōura region or within the Kaikōura MPA, showing an apparent lack of foraging in the area close to the colony. Despite birds remaining at sea for two to 15 days, no bimodal

pattern was detected between foraging trips which may be due to the small sample size. I was able to determine variation in diving depths between coastal and oceanic locations. My results also identified nocturnal rafting locations as occurring predominantly in deep oceanic waters. A significant difference was detected in bathymetry between the non-foraging and foraging sites, but no relationship was detected between chlorophyll *a* concentration and foraging behaviour

I found the tracked birds flew south-southeast from the Kaikōura Peninsula colony during the January chick-rearing period (Fig. 4.1). The overall direction of travel was along the Kaikōura and Canterbury coastlines towards Banks Peninsula or out over the deep oceanic water towards the Mernoo Bank area. It has been shown that Cory's shearwater (*Calonectris diomedea*) will utilise tail and crosswinds to aid in soaring and avoid headwinds (Paiva et al. 2010a), but the small number of birds I tracked did not allow me to compare the flight paths with wind direction or wind speed. Interestingly, over the three-week study period, the Hutton's shearwaters flew similar flight paths independent of departure date (Fig. 4.2), and the return flight paths of four individuals were reasonably direct, with only a few deviations, indicating that any effects of variation in wind direction and speed may have little impact although this needs to be investigated further. Some of the Hutton's shearwaters did make short stopovers along the way. These brief periods may have been used for investigating an area, foraging, resting or to join up with other birds.

Flocks of Hutton's shearwater are regularly seen just offshore from Kaikōura, and the general belief has been that the birds are foraging within the coastal region (Harrow 1976; Marchant & Higgins 1990; Taylor 2000). In contrast to local expectations, only

three birds remained within close proximity to the colony, and only one bird stopped briefly within the protected marine reserve for a short period of time (Fig. 4.3). Similar results were observed for the Scopoli's shearwater (*Calonectris diomedea*), which also lacked overlap in distribution with a previously designated conservation area in Tunisia. In this instance, recommendations were made to extend the marine conservation boundaries (Grémillet et al. 2014). Alternatively, research on black-legged kittiwakes (*Rissa tridactyla*) and Balearic shearwater (*Puffinus mauretanicus*) found that over 50% of resting and foraging activities overlapped with existing MPAs that either surrounded or were adjacent to the breeding colonies (Meier et al. 2015; Ponchon et al. 2017). By identifying areas which are regularly frequented by the Hutton's shearwater, consideration can be made with regards to the extension of a pre-existing MPA or the recommendation for the establishment of a new MPA area (Taylor 2000). This knowledge will also allow for the investigation of whether there is any foraging conflict with commercial fishing activities and for any potential competition with available fish stocks (Taylor 2000; Pichegru et al. 2010). The current placement of the Kaikōura MPA does not appear to be providing a large enough area or sufficient protection for this particular species.

Foraging patterns and day-time behaviour

I found no evidence of a bimodal foraging pattern within the Hutton's shearwater. Some shearwater species (short-tailed, sooty, little and Cory's shearwater *Calonectris diomedea*) have been classified as bimodal with foraging trips ranging between short and long durations (1–3 and 5–17 d) (Granadeiro et al. 1998; Weimerskirch 1998; Weimerskirch & Cherel 1998; Booth et al. 2000; Baduini & Hyrenbach 2003; Ryan et al. 2017). The lack of a bimodal pattern may be partly due to the low samples size.

Foraging locations could not be established for a number of birds due to battery failure, and unfortunately, these incomplete tracks prevented me from establishing the complete extent of their foraging range. Where birds went during trips over two to four days are unknown, but the GPS fixes indicate that the birds may have continued south-southeast (Fig. 4.1; e.g., birds A and E). It has been proposed that long foraging trips are used by the adults to maintain body mass and that birds return in better condition after long trips than short foraging trips (Baduini & Hyrenbach 2003). It has been suggested that the bird's body condition determines the type of trip undertaken more so than the breeding stage or a chick's dietary requirements (Weimerskirch & Cherel 1998). During the chick-rearing period, adults may rely on body reserves while foraging closer to the colony over shorter periods of time to provision their chick (Weimerskirch & Cherel 1998; Cleeland et al. 2014).

This study was focused on assessing where the birds were diving, more so than the depth of dives (see Chapter 2). My results did indicate that Hutton's shearwater utilised areas at some distance from the coastline (260 km) and in areas of deep water (1780 m). In contrast, Balearic shearwater breeding on Mallorca Island spent 92% of their tracked movement within 20 km of the colony or Spanish coastline and within waters less than 100 m (Meier et al. 2015). Alternatively, short-tailed shearwater in Tasmania travel as far as the Antarctic Divergence and west of Bouvetøya Island to forage and provision chicks (Klomp & Schultz 2000; Cleeland et al. 2014; Ryan et al. 2017).

I found the Hutton's shearwater spent the majority of their foraging trip within the Pegasus Bay, Mernoo Bank (western end of Chatham Rise) and Canterbury Bight

areas (Fig 4.7, 4.8). Within these areas, diving depths and dive durations varied between and within each foraging site. For example, the deepest dive recorded was a maximum of 16.4 m which is considerably less deep than the 35 m (incubation) or 26.8 m (chick-rearing) recorded during the 2014–15 breeding season (see Chapter 2). Paiva et al. (2010a) found Cory's shearwater dived deeper and longer within an oceanic environment whereas shorter shallower dives were undertaken in a coastal region. My small dataset does not allow the identification of any such pattern.

Nocturnal-rafting behaviour

I found several rafting locations where birds remained overnight (Fig. 4.10). All of these locations were over deep water except for two individuals within the Canterbury Bight area (Table 4.2) or when leaving or returning to the colony (see below). These areas may indicate where birds were diving before dusk or where they would commence foraging when suitable light returned. Hutton's shearwaters are visual predators and are not generally known to dive at night (see Chapter 2). Surprisingly, although day-time diving events were recorded within the Pegasus Bay area, no night-time rafting behaviour was detected within this area. It has been suggested that Manx shearwater shift to shallower water at night-time (Guilford et al. 2008), whereas I found the Hutton's shearwater tended to raft in deeper oceanic waters.

Rafting behaviour in Hutton's shearwater has regularly been observed where individuals congregate offshore (~1 km), especially during the late evening before the birds return to their breeding colonies (Harrow 1976). As evening approaches individuals form large rafts until night-fall whereby they fly inland en masse. Interestingly, it has been reported that the breeding population of Manx shearwater

raft at a greater distance from shore than the non-breeding individuals (Guilford et al. 2008). As I only recorded four return tracks and detected only one individual with evening coastal rafting behaviour near the Kaikōura Peninsula, I am unable to speculate on the Hutton's shearwater near-colony rafting behaviour.

Chlorophyll a and bathymetry

New Zealand's continental shelf is generally narrow and boarded by extensive submarine plateaus in the northwest and southeast (Leathwick et al. 2006). The Subtropical Front flows around the bottom of the South Island before heading north along the east coast and out along the Chatham Rise. This area is associated with mixing of subtropical and sub-Antarctic waters and is associated with high primary productivity (Leathwick et al. 2006). These rich areas of surface water are located over depths of 800–1000 m, and the extensive canyon system off the Kaikōura Peninsula includes areas within this bathymetric range. The Kaikōura coast is unique in its variable bathymetry due to the submarine canyon cutting into the continental shelf (Lewis & Barnes 1999; De Leo et al. 2010). This is expected to create an area of high productivity, convergence and concentration of potential prey for foraging seabirds, e.g., the red-billed gull (*Larus novaehollandiae scopulinus*) (Bradford 1972; Mills et al. 2008). It was expected that the Hutton's shearwaters would be feeding in areas of high productivity and therefore the canyon would be an obvious location. However, this was not observed when I considered chlorophyll *a* concentration levels and bathymetry as indicators for foraging locations.

I found the Kaikōura Peninsula chlorophyll *a* concentration was not significantly different to the areas in which Hutton's shearwaters have been found foraging (Fig.

4.9; Table 4.2). My results show Hutton's shearwater foraged predominantly within locations at some distance from the colony and not within the near-shore Kaikōura region (Baduini & Hyrenbach 2003; Freeman et al. 2010; Dias et al. 2011). Baduini and Hyrenbach (2003) found higher chlorophyll *a* concentration levels within long foraging trip areas for bimodal species of Procellariiforms. They also suggest that chlorophyll *a* productivity was equally predictable within short and long trip foraging areas. Similarly, when the chlorophyll *a* concentration from foraging sites of the black petrel (*Procellaria parkinsoni*) were considered, no relationship was detected between the primary productivity and foraging location (Freeman et al. 2010). If chlorophyll *a* alone were a proxy for identifying foraging locations, I would expect more time would have been spent feeding within close proximity to the Kaikōura Peninsula. I conclude that the primary productivity is insufficient to suggest possible foraging behaviours or strategies.

I also found that the bathymetry of the Kaikōura Peninsula site is significantly deeper on average compared to the Canterbury Bight, Pegasus Bay and Mernoo Bank areas, and this variation in bathymetry may influence foraging behaviour (Table 4.2). The Hutton's shearwater appear to prefer shallower waters around coastal areas and over the Mernoo Bank. These areas are associated with eddies and wind-induced up-wellings due to the mixing of currents and the variation in bathymetry (Vincent et al. 1991; Shaw & Vennell 2000; Reynolds-Fleming & Fleming 2005). These environmental conditions may aid in site fidelity and provide a more predictable food resource (Phillips et al. 2017). For example, the black petrels forage in close proximity to the shelf-breaks along the continental shelf off the North Island of New Zealand (Freeman et al. 2010). Alternatively, sooty shearwater and short-tailed

shearwater prefer colder, deeper, more productive waters which are driven more by oceanic processes (Shaffer et al. 2009; Cleeland et al. 2014). Although this is a small dataset, it appears that the underlying bathymetry and ocean shelf-break or slopes may play a part in foraging behaviour.

During a study in 1996, an increase in Hutton's shearwater abundance was observed off the eastern coast of Banks Peninsula (Hawke 1998). Flock numbers increased with the greater distance from shore. When seabird numbers were compared to the internal waves (sub-surface waves which may entrain zooplankton and small fish) and convergent fronts or tidal plumes (noticeable foam or seaweed accumulation) within 7.3 km from shore, no correlation between bird occurrence and oceanic features were apparent (Hawke 1998). These results indicate that Hutton's shearwater may be more pelagic than benthic foragers. I was not able to investigate the diet of the birds I tracked, but this species is believed to feed on small fish, crustaceans and squid (see Chapter 3) (Tarburton 1981; West & Imber 1985).

Here, I investigate two factors which may influence Hutton's shearwater behaviour and foraging locations. First, the recent earthquake event; and second, commercial fishing activity**.**

Earthquake

Unfortunately, Kaikōura was affected by a magnitude 7.8 earthquake on 14 November 2016 which caused extensive seabed deformation (≤ 7 m) along 110 km of coastline, with mountain and river outwash, and sediment slips into the Kaikōura Canyon (Lewis & Barnes 1999; Clark et al. 2017). It is unknown how this event and

subsequent changes to the Kaikōura ocean environment may have affected and influenced the Hutton's shearwater foraging behaviour. Through the evolution of the species (Holdaway 1999; Holdaway et al. 2001), earthquake events would not be unique. Due to the fact that all chicks successfully fledged and I saw little variation in adult weight change during the study, I believe the birds were able to cope with this event, and that Hutton's shearwaters may be flexible in foraging strategies and that they have the ability to adapt within a short space of time (Paiva et al. 2010b). This behaviour may allow this species to be more flexible to environmental changes (Paiva et al. 2010b; Paiva et al. 2013a). This study has provided a good baseline for future GPS tracking analysis, and to determine if the patterns of at sea behaviour change as the marine environment in the Kaikōura area recovers over the coming decades.

Fisheries

The locations in which the Hutton's shearwaters are foraging are important fisheries areas of New Zealand. Situated east of the Canterbury Bight and Pegasus Bay, and starting in the Mernoo Bank area is the western edge of the Chatham Rise. These areas are high in species richness and are areas of intense commercial fisheries (McClatchie et al. 1997; Francis et al. 2002; Leathwick et al. 2006).

Hutton's shearwaters do not readily associate or follow boats, but they can be easily approached if in a feeding frenzy or rafting in groups (Marchant & Higgins 1990; Wood 1993). This behaviour could lead to potential issues. Firstly, large-scale purse seining fishing occurs inshore of the Banks Peninsula region (Taylor 2000). This fishing style can force smaller fish to the surface, thereby increasing the availability of food and increasing the risk of being trapped as by-catch. Hutton's shearwater may

forage on these surfacing prey species or undertake pursuit dives (Marchant & Higgins 1990). Secondly, there are also potential by-catch issues with commercial fisheries, placing these seabirds at a greater risk (Taylor 2000; Richard et al. 2011). Two by-catch occurrences have been reported within the Kaikōura region. Individuals were drowned in nets set off the Kaikōura Peninsula (nine birds in August 1980 and 50 individuals in October 1984) within approximately 2–4 m of water (Tarburton 1981; West & Imber 1985). Lastly, deep sea-trawling activity occurs off the Canterbury and Banks Peninsula coastline and Chatham Rise (Taylor 2000; Francis et al. 2002; Pierre et al. 2013). Marchant & Higgins (1990) suggest Hutton's shearwater may take advantage of offal products released overboard from fishing vessels during the breeding season. However, during a feeding study undertaken in New South Wales, Australia (August) involving various seabird species, it was found that the Hutton's and fluttering shearwater (*P. gavia*) were not interested in the fish offal or animal fat products thrown overboard; whereas the short-tailed (*P. tenuirostris*), flesh-footed (*P. carneipes*), wedge-tailed (*P. pacificus*) and sooty shearwater readily took the supplied bait (Wood 1993). This variation in Hutton's shearwater behaviour needs further investigation.

Future research

During this study, I investigated the behaviour of successful breeding birds; however, this southerly distribution may not be consistent with non-breeding birds or failed breeders. These birds may have different nutritional requirements and could be exploiting other areas (Guilford et al. 2008). Alternatively, if I had tracked individuals during the pre-laying exodus or incubation period, northerly or easterly flights may have been identified (Cleeland et al. 2014). In addition, we have little knowledge of

their interaction with commercial fisheries and the potential implementation of new MPA areas. This research has provided a good baseline on breeding adults, but future research into these other areas is required to provide a more complete picture.

Conclusion

This study provides important insight into the foraging behaviour of the Hutton's shearwater. The use of light-weight TDR loggers and GPS trackers has allowed me to gain information on where these birds went to forage during the chick-rearing period. Even with the lack of complete tracks, I have obtained a snap-shot of their at sea behaviour over the vast open water. I found an overlap between the various individuals and different foraging locations that were situated south of the breeding colony. Unfortunately, due to the November 2016 earthquake, the observed tracking behaviour may have been altered, or other environmental factors may have influenced these results (Paiva et al. 2013b). At present, I only have tracking data for the post-earthquake period. At this time, these results do not indicate that the birds are remaining in the Kaikōura region or utilising the Hikurangi Marine Reserve (MPA). Similarly, the use of more northern and eastward locations may occur during the pre-breeding, incubation or chick-rearing periods but were not detected during this study.

Providing safe foraging areas at sea can be difficult due to wide-ranging areas that a species utilise. The marine environment is subject to increasing pressure from fisheries, tourism and deep-sea oil exploration. Certain areas may be most beneficial for different aged birds (immature vs breeding birds) or breeding stages (pre-laying exodus, incubation, chick-rearing) and foraging trip type (short or long). For the effective implementation of new protection sites a fuller understanding is needed of

the foraging areas and site utilisation by these wide-ranging birds. More investigations are now required to address the influence of the earthquake event and other climatic events (e.g., El Niño and La Nina), and to further our knowledge of their foraging behaviour during the incubation and non-breeding periods.

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Hutton’s shearwater chick sitting in a nesting box in the Kaikōura Peninsula colony, 12 February 2017 (photo by DG Bennet).

Chapter 5

Isotopic evidence of endogenous nutrient contribution in Hutton's shearwater (*Puffinus huttoni*) reproduction

Abstract

Stable isotope analysis is an effective tool to investigate the energetic costs of reproduction. By assessing dietary pathways, the relative contribution of endogenous and exogenous resource allocation can be compared. Using feathers collected from adult and nestling Hutton's shearwater at various times during the breeding season, I found the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of natal chick feathers were significantly different to the adult feathers experimentally induced during the breeding season. I found the nutrients collected by Hutton's shearwaters during the non-breeding period were predominantly used to produce the egg and consequently the hatchling and its first natal feathers. However, as the breeding season progressed and the adults fed their chicks, subsequent chick feather samples became progressively similar to the local environment and induced adult feather samples. Based on my results, I conclude the Hutton's shearwaters are predominantly endogenous breeders early in the breeding season, but then rely on exogenous resources as their chicks mature.

Introduction

Reproduction is energetically expensive, especially for species with low fecundity that produce only a single or a few eggs (Astheimer & Grau 1990; Hamer et al. 2002).

Many seabird species lay eggs which are large relative to the female's body size (Whittow 2002). Acquisition of resources required for the reproductive period can involve both increased foraging in the breeding period but also nutrient storage during the non-breeding period (Jonsson 1997). Jonsson (1997) suggests energetic stockpiling in the non-breeding period can be advantageous when: 1) food resources are scarce during breeding (e.g., egg production, incubation and self-maintenance); 2) breeders are reliant on high food demands early in the season; 3) there is variability in foraging success and metabolic demands; 4) predation risk is increased while acquiring energy and being more actively conspicuous or less agile while carrying an egg; and 5) breeding constraints (nesting) reduce foraging time. If any of these conditions arise, reproductive success could be affected by the ability of individuals to store energy on the non-breeding grounds prior to the breeding season.

Dietary pathways have previously been investigated through gut content analysis, and have included studies on albatross, petrel and shearwater species (Hobson 2006; Phillips 2006; Colabuono & Vooren 2007; Spear et al. 2007; Bester et al. 2011). More recent advances in isotopic analyses have enabled researchers to indirectly measure diet in species such as Balearic shearwater (*Puffinus mauretanicus*), little penguins (*Eudyptula minor*) and glaucous-winged gulls (*Larus glaucescens*) (Blight et al. 2014; Kowalczyk et al. 2014; Meier et al. 2016). Isotopic ratios of nutrient allocation have also been traced between parental and chick tissues in several species such as the common eider (*Somateria mollissima*), pink-footed goose (*Anser brachyrhynchus*), common tern (*Sterna hirundo*) and Caspian tern (*Sterna caspia*) (Hobson et al. 2000; Hobson et al. 2015; Jaatinen et al. 2016; Klaassen et al. 2017). Common and Caspian tern breeding around Great Slave Lake use marine derived protein in yolk formation,

and common terns use lipids derived from the marine food web for whole egg production (Hobson et al. 2000). Heavy eider females use stored reserves to produce the egg yolk early in the season and progressively change to locally acquired nutrients to produce the last eggs during the breeding season (Jaatinen et al. 2016). Light-weight eider females do not vary their allocation pattern over the breeding season and rely largely on local nutrients. In addition, the northern Baltic common eider showed endogenous reserves being used in egg yolk formation but not in albumen (Hobson et al. 2015). The Svalbard-breeding pink-footed goose forms well-developed follicles while in flight to the breeding grounds and uses between ~50-100% endogenous nutrients in yolk formation (Klaassen et al. 2017).

When birds forage within isotopically distinct environments (e.g., marine vs. terrestrial), it is possible to track the change in isoscape and determine the exogenous or endogenous contribution to their reproductive effort. The relative importance of these two sources of energy to reproduction broadly define capital vs income investment (Hobson 2006). Capital investment refers to mobilised endogenous reserves (muscle protein and lipids from fat storage) that have been obtained in a different isoscape (e.g., non-breeding period, *en route* or anywhere prior to breeding) than the breeding locations and have been utilised to produce the different egg components (shell, albumen and yolk) (Jonsson 1997; Hobson 2006). Income investment refers to exogenous breeders who adjust their food intake during the egg development stage without relying on stored lipids or proteins (Jonsson 1997). Nitrogen from prey items are typically assimulated into protein within the consumer, whereas carbon can be used to form different components, including proteins, lipids and glycogen (Podlesak et al. 2005; Hobson 2006). There are several advantages and

disadvantages for each of these strategies. Endogenous breeders require the ability to accumulate and store sufficient resources which are energetically expensive to maintain but will provide insurance against the variable conditions (e.g., weather, lack of prey, competition) they may encounter within the breeding environment (Jonsson 1997). By carrying this increased body mass, an individual may be more exposed to predatory risk through increased foraging exposure and flight costs. Exogenous breeders can avoid these costs but only if the breeding environment is predictable and without resource limitations (Jonsson 1997).

Several studies have investigated the nutrient pathways in waterfowl and gulls (Gauthier et al. 2003; Hobson et al. 2004; Sénéchal et al. 2011). Variation was found in nutrient allocation between income vs. capital breeders and the egg laying order of a clutch. For example, Gauthier et al. (2003) found greater snow geese are prodominantly income breeders, but late laying females will invest more endogenous reserves in the development of eggs later in the clutch laying period than early layers. Similarly, a slightly higher $\delta^{15}N$ values were detected in the last laid egg compared to the first egg in the common eider (Sénéchal et al. 2011). Alternatively, no difference was detected between the sequential laying of eggs in redhead ducks (*Aythya americana*) (Hobson et al. 2004). Only a few studies have addressed maternal nutrient transfer in Procellariiformes (Quillfeldt et al. 2005; Gladbach et al. 2007; Bond & Hobson 2015). For example, Wilson's storm petrels (*Oceanites oceanicus*) are income breeders and use resources collected close to the breeding colony (Quillfeldt et al. 2005; Gladbach et al. 2007). In contrast, Leach's storm petrel (*Oceanodroma leucorhoa*) utilise endogenous resources to lay a second or third replacement egg due to egg loss (Bond & Hobson 2015).

Hutton's shearwaters forage within isotopically distinct breeding and non-breeding locations (see Chapter 3), allowing comparisons to be made between the isotopic values of endogenous and exogenous nutrients/resources. Hutton's shearwater is an endangered endemic species that return to their New Zealand breeding grounds during late August (Cuthbert & Davis 2002). Breeding pairs only produce a single egg, starting in late-October and the chicks hatch from late December (Cuthbert 2001). Through using feathers as a proxy of nutrient utilisation, in this chapter, I compare adult isotope ratios during the non-breeding and breeding period with isotope ratios at various stages in nestling feather growth during the chick-rearing period (Cherel et al. 2000; Cherel et al. 2005). First, I aim to consider the endogenous nutrient contribution to Hutton's shearwater egg production by comparing the adult non-breeding feather isotopic composition to the composition of natal down at hatching. This will signify the adult diet when the egg, particularly the natal feathers, were formed. Next, I assess how the isotope ratios change between the natal down to the secondary down and fledging feathers, both of which grow as the nestlings are fed by the adults on local prey. Finally, I compare the isotope ratios of adult feathers grown on the non-breeding grounds with that experimentally induced (and thus grown) on the breeding grounds. Together, these objectives will allow me to assess the relative contribution of endogenous vs exogenous resources to egg production and early nestling growth.

Methods

Ethical statement

This study was performed with permission of the Department of Conservation (DOC). Permits were provided by the DOC (WAA-38708-FAU) and the University of Canterbury Animal Ethics Committee (2014/20R).

Feather collection

During the 2014–15 breeding season, Hutton's shearwater feathers were collected from the coastal Kaikōura Peninsula (Te Rae O Atiu, ~80 m.a.s.l) colony for stable isotope analysis. Feather samples were collected from seven females, five males and seven chicks at different times during the breeding season. Breast feathers and a tail feather (rectrices R5) were removed from each breeding adult during the incubation period (mid November-early December 2014). The birds arrive on the breeding grounds with these feathers fully formed, indicating they were grown on the non-breeding grounds during the pre-nuptial moult. From these samples, only analyses of the female feather were used to establish the non-breeding $\delta^{13}C$ and $\delta^{15}N$ values, as only they would be potentially contributing nutrients to chick natal down through the egg composition (Gladbach et al. 2007). Induced replacement adult tail feathers were then collected once fully regrown from all adults during January 2015; these were used to indicate the breeding season isotope signature as the replacement feathers were grown while the birds were in the breeding grounds. Chick natal down feathers (protoptile; hereafter 'natal') were collected within a few days of hatching and used to represent the maternal resources in the egg or nutrient signature from which the adult female used to produce the egg (Richdale 1943; Gladbach et al. 2007). Hutton's

shearwater chicks grow a secondary down (mesoptile; hereafter 'down'), and samples were collected from the breast area (approx. 3–4 weeks after hatching). This represents the diet provided by the adults (Richdale 1943; Dunlop 2011). Lastly, fledging breast feathers (teleoptile) were collected (10 weeks after hatching) before the chicks left the colony (Percival 1942; Harrow 1976).

Isotope analyses

Feathers were cleaned of surface contaminants using 2:1 chloroform:methanol, rinsed in MilliQ water (nano-pure deionised) and air dried for 48 hr in a fume hood until completely dry. The natal down feathers were not cleaned due to the concern of sample loss, as they were exceptionally fine and light-weight. To assess any effect of not cleaning the natal down feathers, a sample of cleaned secondary down feathers for each chick was compared to a sample of uncleaned secondary down. No significant difference was detected between the carbon (t = 0.54, d.f. = 6, [CI –0.11, 0.17], P = 0.61) or nitrogen isotopic compositions (t = –0.23, d.f. = 6, [CI 0.10, 0.08], P = 0.83). Feather sections were weighed 500 micrograms (± 100 μg) and placed into tin capsules (DEA Laboratories 8mm x 5mm) for SIA (see Chapter 3).

Nest identification and feather type (breeding tail, non-breeding tail and breast feathers from adults; natal, down and breast feathers from nestlings) effects on feather isotope values were estimated in a linear mixed-effects model framework (R package *lme4*, version 1.1-7, Bates et al. 2015), using R version 3.3.0 (R Core Team 2017). Separate models were assumed for carbon and nitrogen isotope compositions. The effect of individual identification within each nest was included as random effects on the intercept ('band'), taking the correlation between repeated measurements on the

same individuals into account. Model selection was performed using the Akaike's Information Criterion (AIC_c) to determine the best model (R package *boot*, version 1.3-18). A model was identified as the best model when it had the lowest AIC_c value with a difference >2 compared with the second best model. I used a parametric bootstrap to estimate the confidence intervals (R package MuMIn, version 1.15.6). Checking whether the confidence intervals at a particular alpha-level include zero assessed test significance. Negative and positive values showed the direction of the statistical difference. Differences in $\delta^{13}C$ and $\delta^{15}N$ between the cleaned and uncleaned down were examined by Student's T-test. A Pearson product-moment correlation coefficient was computed to assess the relationship between the natal feather composition and hatch date. Unless otherwise stated, all values are presented as predicted 95% confidence intervals. All graphs were produced using Grapher12.

Results

Hutton's shearwater adult breeding (male and female tail), non-breeding female (tail and breast) and chick (natal, down, and breast) feather $\delta^{13}C$ and $\delta^{15}N$ values for all individuals are shown in Figure 5.1. Hutton's shearwater chicks hatched over a 26 day period (20 December 2014–15 January 2015; Table 5.1), but the isotopic composition of the chick feathers did not change over this time. There was no correlation between hatch date and either the $\delta^{13}C$ natal feather composition ($t_5 = –0.87$, $r = –0.36$, $P = 0.43$) and $\delta^{15}N$ natal feather composition ($t_5 = 1.82$, $r = 0.63$, $P = 0.13$).

Table 5.1 Summary of hatching order and stable isotope compositions ($\delta^{13}C$ / $\delta^{15}N$ values) for Hutton's shearwater natal feathers during the 2014–15 breeding season. Band and Nest refer to individual identification and nest site for each bird sampled.

Date	Band	Nest	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
20/12/14	X19650	N21	-16.29	13.80
21/12/14	X19647	N46	-16.44	14.03
26/12/14	X19762	N70	-17.70	14.84
27/12/14	X19764	N97	-16.12	14.33
28/12/14	X19649	N51	-16.57	14.36
06/01/15	X19763	N59	-16.57	14.42
15/01/15	X19648	N41	-17.55	14.74

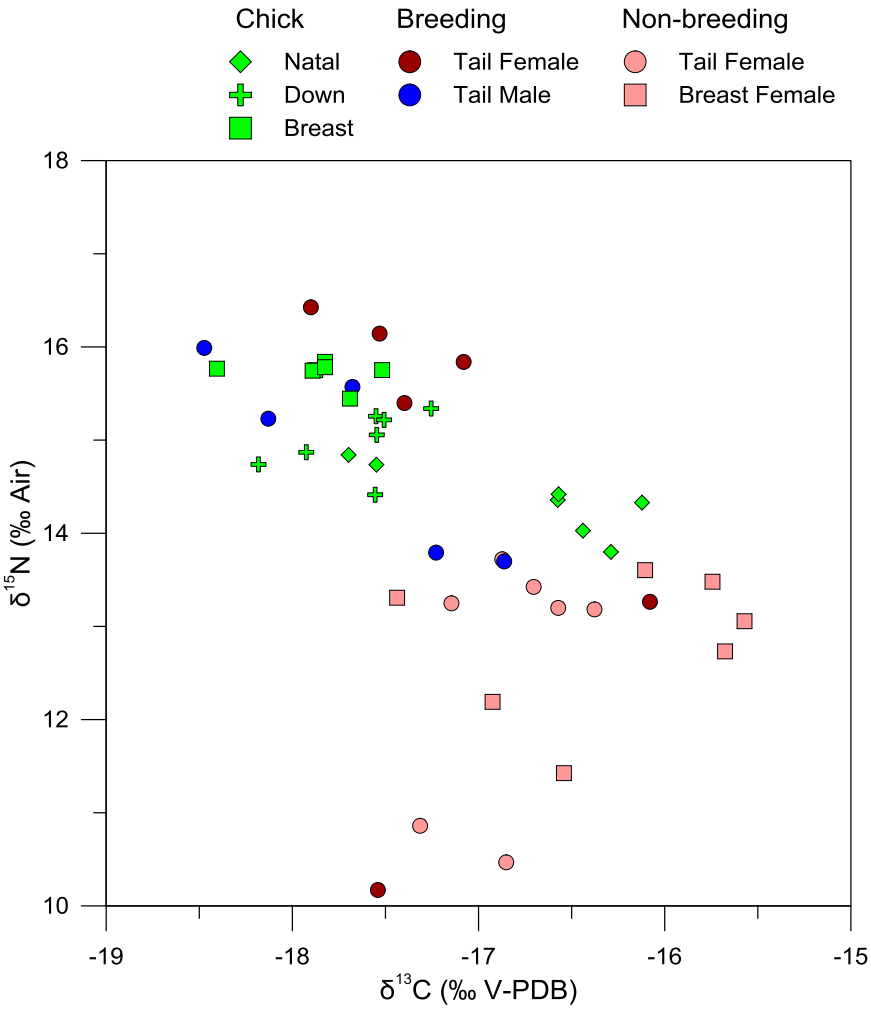

Figure 5.1 Stable isotope compositions ($\delta^{13}C$ / $\delta^{15}N$ values) for Hutton's shearwater chick, adult breeding and adult non-breeding feathers. Each symbol represents a single individual's feather sample from a total of seven nests.

I observed a negative shift in the average $\delta^{13}C$ values and a positive increase in the average $\delta^{15}N$ values between each chick feather sample (Table 5.2). I found the $\delta^{13}C$ values for the natal feathers were mostly clumped around –16.0 to –16.5 ‰ but two individuals were less enriched with values around –17.6 ‰ (Figure 5.1; Figure 5.2: N41 and N70). These two individuals were the third and last chicks to hatch, and were more similar to the isotopic composition of adult feathers from the breeding season. I also identified two males and two females (1/3rd of the sample) with induced tail feathers that were more similar to the non-breeding isotopic composition (Figure 5.1; Figure 5.2: N41, N51, N70 and N97).

Table 5.2 Summary of the stable isotope compositions ($\delta^{13}C$ / $\delta^{15}N$ values) for Hutton's shearwater adult feathers grown during the breeding and nonbreeding seasons and three types of chick feathers (natal, down and breast) from the 2014–15 breeding season (mean ± CI).

Sample	*n*	$\delta^{13}C$ (‰)	Range (‰)	$\delta^{15}N$ (‰)	Range (‰)
Chick					
Natal	7	-16.75 ± 0.46	-17.70 to -16.12	14.36 ± 0.27	13.80 to 14.84
Down	7	-17.65 ± 0.23	-18.18 to -17.25	14.98 ± 0.25	14.41 to 15.34
Breast	7	-17.86 ± 0.24	-18.41 to -17.52	15.73 ± 0.23	15.45 to 15.84
Breeding					
Tail Female	6	-17.25 ± 0.25	-17.90 to -16.03	14.54 ± 0.23	10.17 to 16.43
Tail Male	5	-17.67 ± 0.17	-18.47 to -16.86	14.86 ± 0.45	13.70 to 15.99
Non-breeding					
Tail Female	7	-16.83 ± 0.38	-17.31 to -16.38	12.59 ± 0.99	10.47 to 13.72
Breast Female	7	-16.29 ± 0.57	-17.44 to -15.57	12.83 ± 0.68	11.42 to 13.60

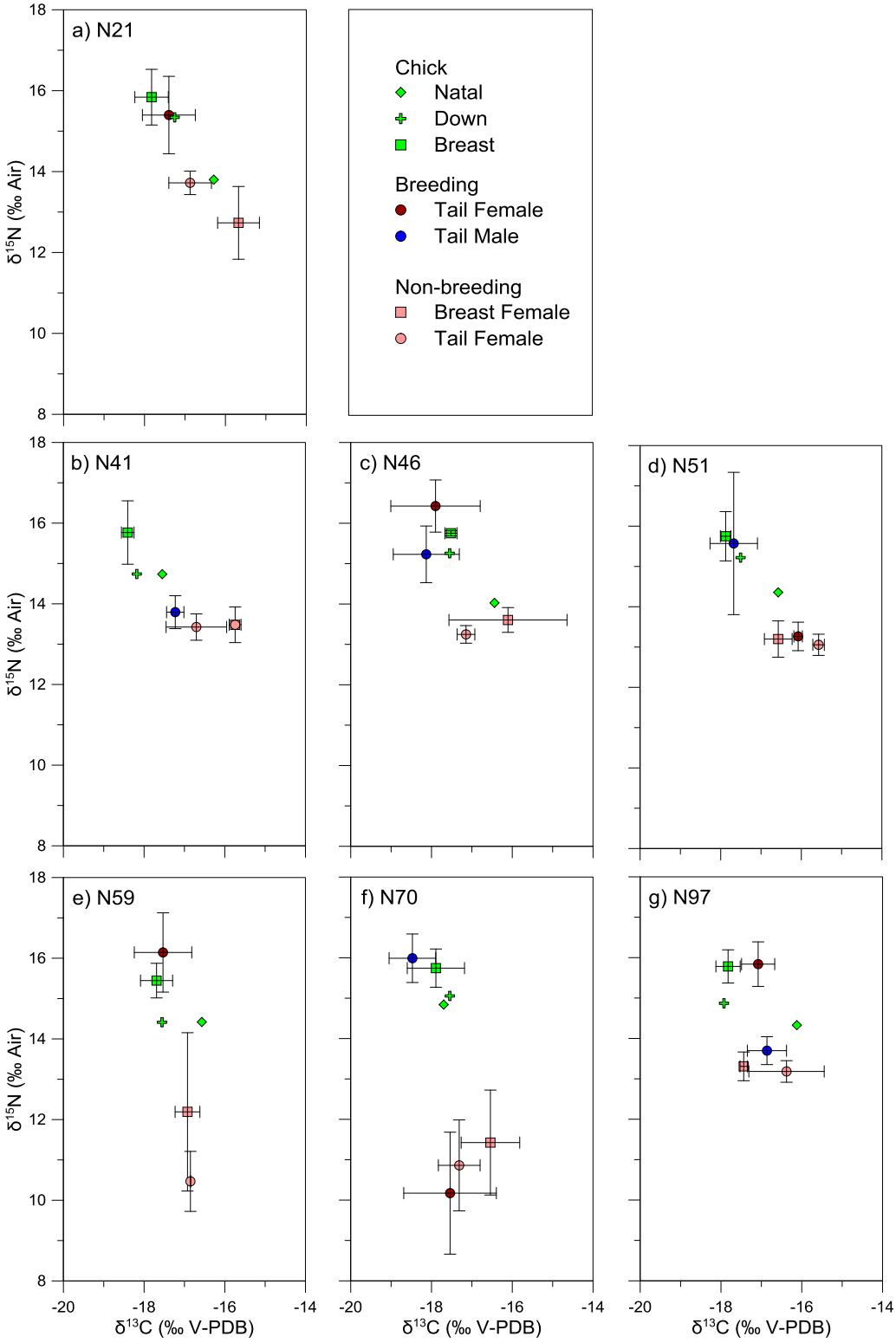

Figure 5.2 Stable isotope compositions ($\delta^{13}C$ / $\delta^{15}N$ values) for Hutton's shearwater adult feathers grown during the breeding and nonbreeding seasons and chick feathers from the 2014–15 breeding season (mean ± CI and individual values). Values for each individual have been graphed separately by nest identification (a-g).

The two best models selected to describe the $\delta^{13}C$ and $\delta^{15}N$ values included 'Feather' as a fixed effect and 'Band' as the random effect (Table 5.3). As expected, I found that the $\delta^{13}C$ and $\delta^{15}N$ values of natal feathers (Std. Est. 0.68, [CI 0.20, 1.24]; Std. Est. –0.36, [CI –1.32, 0.78]; respectively) were not significantly different to the $\delta^{13}C$ values of non-breeding adult tail and breast feathers (Std. Est. 0.54, [CI 0.10, 0.95]; Std. Est. 1.09, [CI 0.66, 1.51], respectively). However, they were significantly different to the $\delta^{15}N$ values (Std. Est. –2.10, [CI –3.04, –1.18]; Std. Est. –1.85, [CI –2.64, –0.84], respectively). A significant difference was also observed between the natal feather $\delta^{13}C$ values and the induced adult breeding tail feathers (intercept; Std. Est. –17.43, [CI –17.72, –17.14]), but no difference was observed between the $\delta^{15}N$ values (intercept; Std. Est. 14.72, [CI 14.00, 15.40]). Similarly, there was no significant difference between the chick down and chick breast feathers ($\delta^{13}C$ Std. Est. –0.22, [CI –0.70, 0.23]; $\delta^{15}N$ Std. Est. 0.27, [CI –0.75, 1.38]; $\delta^{13}C$ Std. Est. –0.43, [CI –0.96, 0.09]; $\delta^{15}N$ Std. Est. 1.01, [CI –0.05, 2.08]; respectively), and the replacement regrown adult breeding tail feathers.

Table 5.3 Comparison of linear mixed-effects models to explain carbon and nitrogen values. Selected models are in bold. 'Band' was used as random variable for all models The fixed effects were: 'Nest' identifying the seven burrows which contained chicks and male and/or female adult occupants; 'Feather' was used for the Chick (natal, down and breast feathers), Breeding (male and female tail feathers) and Non-breeding samples (female and male tail feathers). In one 'Feather' model (indicated by *) 'Nest' was changed from a fixed effect to a random variable and was used as an error term with 'Band'. Log likelihood = natural logarithm of the maximum likelihood for the model; AIC_c = Akaike Information Criterion model score; ΔAICc = difference in Akaike Information Criterion score between models; Weight = Akaike Information Criterion weights.

Model	d.f.	Log Likelihood	AICc	ΔAICc	Weight
Carbon					
Nest + Feather	14	-34.54	110.63	18.73	7.06E-05
Feather	**8**	**-36.01**	**91.90**	**0.00**	**8.23E-01**
Nest	9	-49.57	122.13	30.23	2.25E-07
Feather*	9	-35.99	94.98	3.08	1.77E-01
Null	3	-51.47	109.51	17.61	1.24E-04
Nitrogen					
Nest + Feather	14	-60.02	161.59	12.54	1.56E-03
Feather	**8**	**-64.58**	**149.05**	**0.00**	**8.23E-01**
Nest	9	-75.77	174.55	25.50	2.39E-06
Feather*	9	-64.58	152.16	3.11	1.74E-01
Null	3	-81.71	169.99	20.94	2.34E-05

Discussion

My results show that the Hutton's shearwater natal feather composition was mostly formed from endogenous nutrients, but a mix of endogenous and exogenous sources were used for later-grown down and fledgeling feathers, as well as for induced feathers in adults. I found the chick down, and breast feathers progressively became similar to the adult regrown tail feathers and were largely formed using the food resources available to adults on the breeding grounds. I conclude that the Hutton's shearwater is mostly a capital breeder during the production of eggs, but will use a mixed capital/income strategy over the breeding season as the chicks mature. This mixed strategy may provide some protection against poor winter resource acquisition, although how this may aid in reproductive success is unknown.

As the natal feather composition was comparable to the adult non-breeding tail and breast feather composition, my research suggests that female Hutton's shearwater predominantly use capital investment to produce various egg components and the corresponding isotopic values contributing to the chick natal feathers were either sourced from the winter foraging grounds or en route to the breeding grounds (Hobson 2006; Klaassen et al. 2017). Previous studies support natal feathers being used to establish adult pre-laying diet as the hatchling natal feathers are assimilated predominantly from egg albumen and a small fraction from the lipid-free fraction of yolk (Romanoff & Romanoff 1949; Klaassen et al. 2004; Quillfeldt et al. 2005; Gladbach et al. 2007). Alternatively, four adult tail feathers (two males and two females) regrown during the incubation and chick-rearing period were constructed from isotopic values similar to the non-breeding period (see Chapter 3). This may indicate either that birds are accessing foraging areas during the pre-laying exodus, incubation and chick-rearing period which is masking the capital/income nutrient contribution, or that some individuals are relying partly on endogenous reserves to replace the missing tail feather (Fox et al. 2009).

I found that the date in which eggs were laid did not explain variation in the relative importance of capital vs income investment. Although Hutton's shearwater lay only a single egg, the time period an individual has spent consuming the available prey within the breeding location may have provided an explanation for this inconsistency. For example, Klaassen et al. (2004) found a progressive increase in $\delta^{13}C$ clutch egg values of black-headed gulls (*Larus ridibundus*) during the laying period, and these results were reflected in the hatching chick down. Although I do not know the exact

laying date or total incubation time of each individual Hutton's shearwater egg, I believe that more variability in isotopic composition would have been detected in the natal feathers, if the order in which an egg was laid was important (Morrison & Hobson 2004).

I observed no significant variation between the induced adult tail feathers and the chick fledging feathers, and therefore I assume the adults fed the chicks a diet sourced from similar prey items as consumed during the feather replacement and chick-rearing periods. Furthermore, the isotopic composition of Wilson's storm petrel chick undertail covert feathers and adult feathers grown during the same time period could not be distinguished, and this further supports my findings (Quillfeldt et al. 2005).

I now consider four areas that may have influenced the use of endogenous resources: metabolic demands, migration, food scarcity and breeding colony conditions.

Metabolic demands

My results suggest that Hutton's shearwaters lay down reserves (presumably fat and protein) during the winter period to compensate for the environmental conditions within the breeding colony and foraging sites, and to start the egg yolk formation in the follicles upon their arrival on the breeding grounds (Meijer & Drent 1999; Morrison & Hobson 2004; Mallory et al. 2008; Klaassen et al. 2017). This strategy may be more beneficial than relying on income investment and risking breeding failure or compromise the individual's health. The Hutton's shearwaters' laying resource allocation strategy for the nutrient content of the egg and natal feathers is opposite to that of the greater snow geese (*Chen caerulescens atlantica*). Greater

snow geese are predominantly income breeders and only use increased amounts of endogenous reserves when laying late in the breeding season (Gauthier et al. 2003). In contrast, the Hutton's shearwater switches from capital reserves to income resources and supplements the nutrients required to form the various egg components during the pre-laying exodus period (post-copulation foraging trip) (Warham 1990).

Migration

Hutton's shearwater, like other long-distance migratory species, may use a staging ground before the final flight to the breeding colony (Freeman et al. 2013; Klaassen et al. 2017). Pink-footed geese lay down the egg yolk from capital resources while flying non-stop (~1100 km) between the last staging post and the breeding grounds (Klaassen et al. 2017). During this flight stage, Klaassen et al. (2017) found the pink-footed geese produced well-developed follicles ready for fertilisation and laying, rather than storing reserves in another tissue form which would require catabolism later (Gauthier et al. 2003; Klaassen et al. 2017). It is possible that the Hutton's shearwater may also start forming the egg yolk during the return journey to the colony although this has not been studied directly.

Food scarcity

Unpredictable variation in foraging conditions and the high metabolic and energetic demands on breeding may have a large effect on reproductive success and the individual adult's or chick's health (Jonsson 1997). Similarly, successful breeding could be significantly affected if winter and summer foods are limited (Klaassen et al. 2004). To cope with food scarcity and/or hard environmental conditions (Jonsson

1997), Hutton's shearwater appear to use stored reserves to overcome constraints in the Seaward Kaikōura Ranges and potential ocean prey scarcity.

Breeding colony conditions

When Hutton's shearwaters first return to their alpine breeding grounds, they arrive to snow-covered slopes obscuring their burrows (Harrow 1976; Marchant & Higgins 1990). These birds forage at sea during the day and return nightly awaiting the ground to clear, allowing access to their nests. This may take days to weeks depending on the snow depth (Harrow 1976; Marchant & Higgins 1990). Time constraints during the breeding season will influence breeding success and the use of capital resources. This is especially seen in arctic geese where the breeding season and available food resources are limited (e.g., plant growth) or hard to obtain (e.g., under snow) (Drent et al. 2007; Klaassen et al. 2017). With these varying environmental constraints, it is advantageous for a species to start laying as early as possible (Morrison & Hobson 2004). This is accomplished by building up energy and protein stores so that an individual can prepare for the energetic demands of reproduction (Jonsson 1997). By using capital nutrients, Hutton's shearwater females can lay as soon as their nesting burrow is clear from snow (Harrow 1976; Marchant & Higgins 1990; Cuthbert & Davis 2002) and they are not reliant on obtaining local nutrients. However, as the sampled birds were located within the Kaikōura Peninsula colony where snow does not occur, I do not believe any terrestrial conditions have impacted on the study birds and that these birds are behaving the same as the source alpine colony birds.

Chick survival rate may be reliant not only on the availability of local marine prey (Cuthbert & Davis 2002; Paiva et al. 2013) but also the endogenous/exogenous

contribution to the egg structure. Over a 10 year study on the Hutton's shearwater, more breeding failures were recorded during the incubation than the chick-rearing period (Cuthbert 2001). During a study on lesser black-backed gulls (*Larus argentatus*) eggs laid late within a manipulated clutch contained more water content, fewer lipids and had a lower fledging rate (Nager et al. 2000). Although the Hutton's shearwater lay only a single egg, and the replacement eggs of the Leach's storm-petrel showed no difference in stored energy (Bond & Hobson 2015), variability in egg quality may be affecting chick survival rates. Alternatively, Cory's shearwaters successfully produced eggs despite pre-laying environmental stochasticity, but females foraged at greater distances than normal leading to lower body condition; this greatly increased the incubation pressure of males and lead to egg abandonment (Paiva et al. 2013). Thus, one area for future investigation would be to assess the egg protein and lipid quality in Hutton's shearwater, variation between the origin of the energy and protein source (endogenous/exogenous) and timing of laying and hatch date compared to the chick survival rate. Although the availability of local prey and a chick's growth rate are important factors to consider with regards to chick survival, so might the availability and nutrient contribution obtained during the non-breeding period.

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Hutton's shearwater flying and rafting off the Kaikōura coast, 20 September 2014 (photo by Della Bennet).

Chapter 6
Conclusions

With the discovery of the nesting sites of the Hutton's shearwater in the 1960's (Harrow 1965) and the significant decline from eight colonies to two during the 1980's, research has been focused on invasive pest control at the terrestrial colonies of this species (Cuthbert 2002, Sommer et al. 2009). In contrast, knowledge of the at sea behaviour of Hutton's shearwater has been very fragmentary up until now. Most of our understanding of their at sea has been anecdotal, observational or through by-catch or beach-wreaked birds (Harrow 1976, Warham 1981, West & Imber 1985, Pinkerton 2011). Preliminary diving behaviour has been investigated through the use of simple equipment, such as capillary tubes, and has provided the first estimates for maximum diving depth (36 m) (Taylor 2008), but the breadth of the Hutton's diving behaviour has been unknown. Through gut content analysis, dietary preference has been investigated (Harrow 1976, Tarburton 1981, West & Imber 1985), but foraging locations and how dietary preference may vary over the year or during the breeding season are currently lacking. Although sightings of individuals or small flocks have been made as far as Banks Peninsula, Chatham Rise and Cook Strait (Harrow 1976, Hawke 1998, Pinkerton 2011), most at sea observations of the Hutton's shearwater have predominantly been within the Kaikōura region and the assumption was made that this area was likely to be the main foraging site during the breeding season. Similarly, during the non-breeding period birds are believed to circumnavigate Australia and forage within the Indian Ocean (Warham 1981), but it was not known whether the Hutton's shearwater were income or capital breeders. Until my study, no

previous research has been undertaken to investigate adult dietary contribution to the egg or chick during the chick-rearing period.

Understanding the at sea behaviour of a species is crucial when examining its movements, how they respond to anthropogenic threats and how foraging behaviour may affect population trends, especially in a species which is listed as endangered and nationally vulnerable (Birdlife International 2017, Robertson et al. 2017). The primary purpose of my thesis was to study the Hutton's shearwater's at sea behaviour to widen our knowledge of its diving behaviour, potential diet, and foraging locations. My research has presented new information about the spatial-temporal patterns of diet and foraging in Hutton's shearwater, and this knowledge will help to inform future conservation efforts and provide a baseline of potential interactions with other key environmental factors (anthropogenic issues, climate change and the implementation of any future marine reserve areas). Here I summarise the key results of my thesis, as well as any weaknesses, suggest future avenues for research, and then put my work into context for the conservation of this species.

Summary of main findings

In CHAPTER 2, I explored the diving behaviour of Hutton's shearwater through the deployment of Time-Depth Recorders during the incubation and chick-rearing period, to investigate the depth, duration and frequency of diving by adult breeding birds. I provided the first detailed estimates of diving behaviour for this species and I found significant behavioural differences in diving between the incubation and chick-rearing period, and during different times of the day, indicating temporal and spatial variation. These results suggest that either there may be a difference in energetic

requirements between the breeding and chick-rearing period and this is manifested in different patterns of diving behaviour, or that the differences in diving may indicate a change in the availability of prey. To investigate dietary preference, I tested the isotopic composition of the adult tail feathers in CHAPTER 3, including tail feathers induced to grow on the breeding grounds. I compared the $\delta^{13}C$ and $\delta^{15}N$ values of the diet and feathers, and examined the evidence for sexual segregation during the breeding and non-breeding periods. In fact, I found the isotopic composition of the potential prey species collected from the Kaikōura near-shore region was significantly different from the tail feathers regrown during the breeding period. This significant difference suggests the birds were foraging elsewhere and I proposed a region near Banks Peninsula as a potential location, based on the isotope ratios found in prey collected from this region. Furthermore, the various fractionation models I used (2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$), did not explain the observed isotopic enrichment. I then compared the feathers grown during the breeding and non-breeding period and found a significant difference in $\delta^{13}C$ and $\delta^{15}N$ between seasons. Likewise, a sexual difference was detected within the non-breeding period but not during the breeding season. These findings were opposite to what was expected and did not follow the spatial segregation seen in other species (Forero et al. 2005, Peck & Congdon 2006). To further investigate dietary variation I tracked breeding adult birds through the deployment of GPS units and TDR loggers during the 2017 chick-rearing period (CHAPTER 4). Here, I identified potential foraging locations from diving depth, duration and flight speed data. Even though I had incomplete GPS tracks for most of the individuals, I discovered all birds travelled south from the colony and remained within coastal and oceanic waters within 260 km of Banks Peninsula. Moreover, very little time was spent within the Kaikōura region, suggesting that any

time spent foraging would have been minimal. In fact, a major challenge with this research is the possible implications the Kaikōura earthquake may have had on the Hutton's shearwater behaviour, and whether or not the movements I tracked were due to the birds leaving the Kaikōura due to damage to the marine environment by the earthquakes. In addition, I considered the possible effects of commercial fisheries, chlorophyll *a* concentration and bathymetry on diving behaviour and areas frequented. I speculated that certain areas might be more beneficial for different age groups or breeding stages and this may affect trip length (Alonso et al. 2012, Fayet et al. 2015, Delord et al. 2016). Finally, in CHAPTER 5, I further our knowledge on foraging behaviour and the utilisation of exogenous and endogenous resources from maternal egg nutrients to chick feather formation. Using stable isotope analyses, I found that chick natal feathers were formed predominantly from endogenous nutrients and were significantly different to the adult tail feathers regrown during the breeding period. However, some variability was observed within the chick natal feathers, and I propose this may be due to two females that required some exogenous resources to complete egg formation. Furthermore, as the adults provisioned the chicks and the breeding season progressed, the down feathers and then the fledging breast feathers became more similar to that of the adult feathers. I conclude that the Hutton's shearwaters are predominantly capital breeders but will use a mixed strategy when sufficient endogenous stores are not available. This mixed strategy may provide some protection against poor winter resource acquisition and may aid in reproductive success.

I now discuss the linking factors investigated in the previous chapters of this thesis and the implications of this work. I will then suggest directions for future research and the conservation implications of my research for the Hutton's shearwater.

Linking and significant factors

During my research, I investigated the diving behaviour of the Hutton's Shearwater during two different breeding years. In the 2014–15 breeding season, I studied the diving behaviour of both incubating and chick-rearing adults (n = 6 adults), whereas the second period only covered the chick-rearing period (n = 5 adults, 2017). Although limited sample size prevented detailed analyses between years, I found significant differences in diving behaviour between and within the incubation and chick-rearing periods in the first year of my study. I found maximum dive depths of 35.0 m (incubation, n = 5086 dives) and 26.8 m (chick-rearing n = 8069 dives) during the 2014–15 breeding period whereas the small snapshot of dives recorded (n = 63) during the 2017 chick-rearing period gave a maximum depth of 16.4 m. When the 2014–15 data-set was divided into breeding periods (early and late incubation and chick-rearing), the average dive depth (4.5 ± 0.08 m, n = 8069 dives) and duration (18.0 ± 0.17 s, n = 8069 dives) for the chick-rearing period were similar to the 2017 data (5.5 ± 0.9 m, n = 63 dives and 17.4 ± 2.2 s, n = 63 dives; respectively). Unfortunately, when birds were equipped with both TDR and GPS tracking devices, I found no significant difference in dive depth between the identified coastal and deep oceanic areas (2017, CHAPTER 4). I had hoped to investigate any shorter, shallower dives in coastal waters compared to deeper, longer dives in oceanic waters as seen in Cory's shearwater (Paiva et al. 2010). The lack of variation found in the data removes the possibility of extrapolating the results to the larger breeding data set collected

during the 2014–15 breeding season (CHAPTER 2) because of the low number of TDR dives which corresponded with GPS units.

My results indicate that the Hutton's shearwaters were not predominantly feeding in the Kaikōura region when I compared the isotopic composition of the larval fish and zooplankton with the composition of the induced tail feathers. I proposed that the adult birds may be foraging south around the Banks Peninsula region and this hypothesis was supported by the 2017 GPS tracking data during the chick-rearing period (CHAPTER 4). Although birds are observed at different times during the breeding season between the feather inducement study and the GPS tracking study, I found the chick-rearing adult birds travelled varying distances south of the colony. These flight direction findings not only support the results found in the stable isotope feather analysis (CHAPTER 3), but may indicate that the Kaikōura earthquake had little effect on the bird's behaviour, as there was a two year difference between the isotopic sampling (2014–15; incubation and chick-rearing) and GPS (2017; chick-rearing) data collection periods, that correspond to the time periods before and immediately after the earthquakes.

Limitations of the study

There were a number of limitations in this study that suggest caution is needed in interpreting some of my results. First, although the Kaikōura Peninsula colony was an easily accessible site, because of its recent formation, it currently contained few breeding birds, limiting my ability to obtain larger sample size for some aspects of my study. The age and small size of the colony meant I was also unable to assess differences between the sexes and any effect of age on foraging behaviour. Secondly,

the data was collected over a very short time frame, which means I was unable to assess variation from year to year, a shortcoming that might be particularly important for a seabird species that does have to contend with changes to the marine environment associated with El Niño and the southern oscillation. Finally, during the course of this study, I encountered a number of equipment limitations (logger type, suitable size and weight), and data collection issues (premature battery failure, memory storage and lack of waterproofing). Such technological "glitches" are probably not unexpected when applying new technology to a new species, but I would have been preferable to have had more direct links between the GPS and TDR technology and deployment years. Nevertheless, even with technological problems, I was able to provide a snapshot of the diet and foraging behaviour of Hutton's shearwater that should provide a valuable baseline for future investigations.

Further research and conservation implications

A priority for future research on the Hutton's shearwater is the long-term viability of the species at sea and how it may interact with fisheries. My study has identified that birds fly from the Kaikōura region and spend time at great distances from the colony. Projected by-catch rates by commercial fisheries have estimated that trawler, bottom long-line and surface long-line ships could cause numerous fatalities of Hutton's shearwaters each year (266 birds annually, range 135–482 birds), placing these seabirds at a greater risk (Richard et al. 2011). However, these estimates were based on the birds flying only approximately 70 km from their breeding colonies in Kaikōura to forage (Richard et al. 2011), but as shown in this study (Chapter 4), Hutton's shearwater fly considerably further than predicted and forage within commercial fisheries areas. Whether this leads to greater interactions with fisheries

and higher by-catch mortality needs to be urgently re-assessed (Friesen et al. 2017). Furthermore, the observed time that the tracked Hutton's shearwaters spent within the Hikurangi Marine Reserve was minimal, and thus this protected area provides little protection as a buffer for rafting or foraging birds. Future protected areas and the placement of marine reserves needs further investigation to include the Hutton's shearwater. Taylor (2000) proposed that fishing techniques and harvest levels of fish may be impacting on Hutton's shearwater within the Kaikōura region and that the Department of Conservation should consider the establishment of an inshore Marine Protection Area. This study highlights the need for additional areas situated within oceanic regions and off the coast of Banks Peninsula, including Pegasus Bay, Mernoo Bank and the Canterbury Bight.

My study attempted to identify the current food resources of the Hutton's shearwater at a broad scale using isotopic analyses, but further analysis is required to identify particular prey species. With the development of technology and as camera units become smaller, deployment of video monitoring units may become more feasible to see what the Hutton's shearwater is actually capturing (Moll et al. 2007, Takahashi et al. 2008, Watanabe & Takahashi 2013, Bicknell et al. 2016). Due to the technical constraints and timing, future research should also address the behaviour during the pre-laying, incubation and non-breeding periods. Additional tracking of birds throughout the year would provide a clearer idea of their behaviour and foraging locations as breeders, non-breeders, failed breeders and as juveniles (recently fledged). This study was unable to address questions about the differences in age structure or sex, and these areas need further investigation and access to the alpine colonies may be the best avenue to address these areas.

Ensuring the long-time survival of the Hutton's shearwater requires understanding not only the limitations on their population in the breeding season, but also if any anthropogenic changes have affected their survival on the non-breeding grounds. Indeed, determining the food resources required by the Hutton's shearwater during the non-breeding period is imperative. If increased fisheries or climate change increasingly affects the Indian Ocean, flow-on effects may be seen in the breeding success and future population levels of this species. This is because, as my study has shown, female Hutton's shearwaters usually subsidises the egg nutrient composition with endogenous resources amassed at least in part on the non-breeding grounds, but it is not clear to what extent any short-fall can be compensated by exogenous resources on the breeding grounds and safeguard a female's reproductive success. It is possible that relying on exogenous resources on the breeding ground delays breeding or reduces female condition. Although control of exotic predators is essential within the alpine colonies, dietary effects within the breeding and non-breeding period may have a more substantial effect, and lead to a decline in the population even in the absence of predation risk.

The impact of humanity on the birds of New Zealand has been disastrous, with about half of its endemic species lost since settlement began 800 years ago. The Hutton's shearwater is at risk of joining this tragic history due to elevated rates of predation from exotic predators at its breeding colonies, and ongoing anthropogenic changes to its marine environment. Ensuring the continued survival of this endemic species will not be easy or simple, not the least because so little was known about its behaviour at sea. It is my hope that this thesis has provided some insight into the at sea behaviour

of the Hutton's shearwater that will greatly assist in the future conservation and ensure that the era of extinction in New Zealand has finally come to an end.

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Appendices:

Appendix 1 Linear mixed effects model for dive depth (m), breeding period (early and late incubation and chick-rearing) and time of day (h). Significant variations are indicated in bold.

Depth with Time	Std Est.	2.5%	97.5%
Intercept	2.98	2.50	3.55
PeriodChickL	0.91	0.81	1.02
PeriodIncE	1.36	**1.23**	**1.49**
PeriodIncL	1.18	0.97	1.42
Time11:00	1.20	**1.10**	**1.31**
Time12:00	1.10	**1.01**	**1.21**
Time13:00	1.05	0.96	1.15
Time14:00	1.25	**1.15**	**1.37**
Time15:00	1.39	**1.27**	**1.52**
Time16:00	1.46	**1.33**	**1.61**
Time17:00	1.26	**1.12**	**1.42**
Time18:00	1.11	0.98	1.25
Time19:00	0.89	0.76	1.04
Time20:00	1.40	**1.21**	**1.61**
Time21:00	1.64	**1.50**	**1.81**
Time5:00	1.04	0.88	1.22
Time6:00	1.36	**1.24**	**1.50**
Time7:00	1.36	**1.24**	**1.49**
Time8:00	0.98	0.89	1.07
Time9:00	1.06	0.97	1.15
PeriodChickL:Time11:00	0.93	0.79	1.08
PeriodIncE:Time11:00	0.87	0.75	1.00
PeriodIncL:Time11:00	0.97	0.78	1.21
PeriodChickL:Time12:00	1.26	**1.08**	**1.46**
PeriodIncE:Time12:00	1.02	0.87	1.18
PeriodIncL:Time12:00	0.78	**0.63**	**0.98**
PeriodChickL:Time13:00	1.07	0.91	1.26
PeriodIncE:Time13:00	1.55	**1.33**	**1.81**
PeriodIncL:Time13:00	0.75	**0.60**	**0.93**
PeriodChickL:Time14:00	0.97	0.82	1.14
PeriodIncE:Time14:00	1.25	**1.08**	**1.44**
PeriodIncL:Time14:00	0.67	**0.54**	**0.83**
PeriodChickL:Time15:00	0.83	**0.70**	**0.97**
PeriodIncE:Time15:00	1.02	0.89	1.18
PeriodIncL:Time15:00	0.66	**0.53**	**0.81**
PeriodChickL:Time16:00	0.71	**0.59**	**0.86**
PeriodIncE:Time16:00	1.31	**1.14**	**1.52**

PeriodIncL:Time16:00	0.50	**0.38**	**0.65**
PeriodChickL:Time17:00	0.79	**0.64**	**0.98**
PeriodIncE:Time17:00	1.29	**1.10**	**1.51**
PeriodIncL:Time17:00	0.96	0.66	1.39
PeriodChickL:Time18:00	1.00	0.75	1.32
PeriodIncE:Time18:00	1.31	**1.12**	**1.54**
PeriodIncL:Time18:00	0.79	0.59	1.07
PeriodChickL:Time19:00	1.13	0.84	1.51
PeriodIncE:Time19:00	1.35	**1.12**	**1.63**
PeriodIncL:Time19:00	1.38	0.97	1.95
PeriodChickL:Time20:00	0.93	0.71	1.22
PeriodIncE:Time20:00	0.77	**0.63**	**0.94**
PeriodIncL:Time20:00	0.84	0.63	1.14
PeriodChickL:Time21:00	1.14	0.98	1.33
PeriodIncE:Time21:00	0.68	**0.58**	**0.81**
PeriodIncL:Time21:00	1.08	0.84	1.40
PeriodChickL:Time5:00	1.87	**1.30**	**2.67**
PeriodIncE:Time5:00	1.46	**1.20**	**1.78**
PeriodIncL:Time5:00	1.35	0.85	2.15
PeriodChickL:Time6:00	0.88	0.73	1.05
PeriodIncE:Time6:00	1.10	0.96	1.26
PeriodIncL:Time6:00	1.16	0.89	1.50
PeriodChickL:Time7:00	0.78	**0.67**	**0.91**
PeriodIncE:Time7:00	1.03	0.89	1.19
PeriodIncL:Time7:00	1.08	0.84	1.38
PeriodChickL:Time8:00	1.43	**1.23**	**1.67**
PeriodIncE:Time8:00	1.09	0.93	1.27
PeriodIncL:Time8:00	1.43	**1.08**	**1.91**
PeriodChickL:Time9:00	0.95	0.81	1.12
PeriodIncE:Time9:00	1.06	0.93	1.21
PeriodIncL:Time9:00	1.04	0.81	1.34

Appendix 2 Linear mixed effects model for dive duration (s), breeding period (early and late incubation and chick-rearing) and time of day (h). Significant variations are indicated in bold.

Duration with Time	Std Est.	2.5%	97.5%
Intercept	15.31	14.06	16.66
PeriodChickL	0.99	0.92	1.07
PeriodIncE	1.08	**1.01**	**1.15**
PeriodIncL	1.09	0.96	1.24
Time11:00	1.10	**1.04**	**1.17**
Time12:00	1.07	**1.01**	**1.14**
Time13:00	0.97	0.91	1.03
Time14:00	1.08	**1.02**	**1.15**
Time15:00	1.22	**1.15**	**1.30**
Time16:00	1.16	**1.08**	**1.23**
Time17:00	1.04	0.96	1.13
Time18:00	1.14	**1.05**	**1.24**
Time19:00	0.95	0.86	1.05
Time20:00	1.06	0.96	1.16
Time21:00	0.96	0.90	1.02
Time5:00	1.06	0.95	1.19
Time6:00	1.18	**1.11**	**1.26**
Time7:00	1.15	**1.08**	**1.23**
Time8:00	1.01	0.95	1.07
Time9:00	0.96	0.90	1.02
PeriodChickL:Time11:00	0.93	0.84	1.03
PeriodIncE:Time11:00	0.91	0.82	1.00
PeriodIncL:Time11:00	0.98	0.84	1.13
PeriodChickL:Time12:00	1.09	0.99	1.21
PeriodIncE:Time12:00	1.04	0.94	1.15
PeriodIncL:Time12:00	0.87	0.75	1.01
PeriodChickL:Time13:00	0.92	0.83	1.02
PeriodIncE:Time13:00	1.43	**1.29**	**1.58**
PeriodIncL:Time13:00	0.79	**0.69**	**0.92**
PeriodChickL:Time14:00	0.97	0.87	1.08
PeriodIncE:Time14:00	1.20	**1.09**	**1.32**
PeriodIncL:Time14:00	0.74	**0.64**	**0.86**
PeriodChickL:Time15:00	0.88	**0.79**	**0.98**
PeriodIncE:Time15:00	1.03	0.94	1.13
PeriodIncL:Time15:00	0.78	**0.68**	**0.90**
PeriodChickL:Time16:00	0.86	**0.75**	**0.98**
PeriodIncE:Time16:00	1.32	**1.20**	**1.46**
PeriodIncL:Time16:00	0.70	**0.58**	**0.83**
PeriodChickL:Time17:00	0.95	0.82	1.09

PeriodIncE:Time17:00	1.35	**1.21**	**1.51**
PeriodIncL:Time17:00	0.82	0.64	1.05
PeriodChickL:Time18:00	0.70	**0.58**	**0.84**
PeriodIncE:Time18:00	1.12	**1.01**	**1.25**
PeriodIncL:Time18:00	0.72	**0.59**	**0.88**
PeriodChickL:Time19:00	0.95	0.78	1.16
PeriodIncE:Time19:00	1.20	**1.06**	**1.37**
PeriodIncL:Time19:00	1.02	0.81	1.29
PeriodChickL:Time20:00	0.86	0.71	1.03
PeriodIncE:Time20:00	0.94	0.82	1.07
PeriodIncL:Time20:00	0.95	0.78	1.15
PeriodChickL:Time21:00	0.98	0.88	1.08
PeriodIncE:Time21:00	0.89	**0.80**	**0.99**
PeriodIncL:Time21:00	0.95	0.80	1.13
PeriodChickL:Time5:00	0.99	0.78	1.26
PeriodIncE:Time5:00	1.34	**1.17**	**1.53**
PeriodIncL:Time5:00	1.18	0.87	1.62
PeriodChickL:Time6:00	0.88	0.78	1.00
PeriodIncE:Time6:00	1.18	**1.08**	**1.29**
PeriodIncL:Time6:00	1.10	0.93	1.31
PeriodChickL:Time7:00	0.92	0.83	1.02
PeriodIncE:Time7:00	1.14	**1.03**	**1.25**
PeriodIncL:Time7:00	0.98	0.83	1.15
PeriodChickL:Time8:00	1.22	**1.11**	**1.36**
PeriodIncE:Time8:00	0.95	0.85	1.05
PeriodIncL:Time8:00	1.05	0.87	1.28
PeriodChickL:Time9:00	1.00	0.90	1.11
PeriodIncE:Time9:00	1.15	**1.05**	**1.25**
PeriodIncL:Time9:00	1.11	0.94	1.32

Appendix 3 Linear mixed effects model for the average number of dives per hour (s), breeding status (incubation and chick-rearing) and time of day (h). Significant variations are indicated in bold.

Ave. number dives per hour	Std Est.	2.5%	97.5%
Intercept	47.00	25.65	86.09
TimeInc	0.65	0.28	1.54
Time11:00	1.24	0.54	2.85
Time12:00	1.39	0.60	3.19
Time13:00	0.80	0.35	1.83
Time14:00	1.24	0.54	2.85
Time15:00	1.13	0.49	2.60
Time16:00	0.65	0.28	1.49
Time17:00	0.49	0.21	1.16
Time18:00	0.27	**0.11**	**0.63**
Time19:00	0.20	**0.08**	**0.48**
Time20:00	0.20	**0.08**	**0.46**
Time21:00	1.06	0.46	2.45
Time5:00	0.15	**0.06**	**0.43**
Time6:00	0.58	0.25	1.34
Time7:00	0.97	0.42	2.23
Time8:00	1.16	0.50	2.66
Time9:00	1.10	0.48	2.54
Inc:Time11:00	0.63	0.19	2.11
Inc:Time12:00	0.61	0.18	2.05
Inc:Time13:00	1.11	0.33	3.72
Inc:Time14:00	0.73	0.22	2.44
Inc:Time15:00	1.12	0.33	3.75
Inc:Time16:00	0.81	0.24	2.71
Inc:Time17:00	1.06	0.31	3.60
Inc:Time18:00	2.15	0.63	7.33
Inc:Time19:00	3.70	**1.04**	**13.10**
Inc:Time20:00	2.00	0.59	6.83
Inc:Time21:00	0.62	0.18	2.20
Inc:Time5:00	3.44	0.84	14.19
Inc:Time6:00	1.25	0.37	4.19
Inc:Time7:00	0.88	0.26	2.97
Inc:Time8:00	0.45	0.13	1.52
Inc:Time9:00	0.72	0.21	2.47